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Microsite Requirements for Successful Regeneration in Lowland Northern White-Cedar (Thuja occidentalis) Forests

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MICROSITE REQUIREMENTS FOR SUCCESSFUL REGENERATION IN LOWLAND NORTHERN WHITE-CEDAR (*Thuja occidentalis* L.) FORESTS

by

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An Abstract of the Thesis Presented
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Declines in stands of northern white-cedar (*Thuja occidentalis* L., hereafter cedar) have been observed as both shifts in species composition and reductions in cedar densities, including those stands in lowland sites (Curtis 1946, Boulfroy 2012). While several factors inhibiting cedar regeneration have been identified, a thorough understanding of the conditions associated with the successful establishment and recruitment of regeneration is lacking. Our objectives for the first chapter were to characterize the site conditions associated with live, established seedlings and saplings in lowland cedar stands and to describe how spatial patterns of various cedar size classes relate to these site associations. These objectives were achieved by mapping the seedling, sapling, and overstory communities at 15 lowland cedar stands at five sites in Maine, USA, and examining the fine-scale site conditions (microsites) in which cedar seedlings and saplings occur. Our analyses demonstrated that cedar regeneration tended to occur on elevated microtopographic features (i.e., mounds) while failing to establish in large numbers in small wet depressions (i.e., pits) and interspaces between mounds and pits (i.e., flats); however, this trend was more pronounced for seedlings than for saplings. Volumetric moisture content in these three features was measured was measured once at each site between May 31 and August 27, 2019, and was shown to decrease in the order pits > flats > mounds. Logistic regressions using regeneration

status (live vs. dead) as the response variable further supported the importance of microtopography, as well as canopy openness (greater openness associated with live stems). Neighborhood crowding was also associated with status among saplings (greater crowding associated with live stems), while seedling status did not vary with crowding intensity. In addition, browse on seedlings was associated with dead status. The distinctly clustered spatial patterning found among both seedlings and saplings suggests a dependence on favorable microsites, which exhibit small-scale patchiness within stands. These findings can aid land managers in developing informed plans that allow for canopy openness and diverse microtopography that promote viable cedar populations in these ecologically and economically important forests.

Our overall objective in the second chapter was to assess browsing pressure on tree regeneration in lowland cedar stands. We used observations of seedling and sapling browse from these same 15 stands to explore the following objectives: 1) determine if browse frequency differs by height among cedar seedlings, and 2) assess relative browse impact on common woody species in these stands due to three common herbivores: white-tailed deer (*Odocoileus virginianus* Zimmermann), snowshoe hare (*Lepus americanus* Erxleben), and moose (*Alces alces* Gray). To accomplish the first objective, we determined the percent of cedar seedlings with browse observed on the current year's stems by 10 cm height classes (from 0 to 139 cm), and tested these values against a uniform distribution (equal browse among all classes). Our results showed that browse increased with increasing height class, with seedlings below ca. 50 cm showing a clear positive relationship between increasing height and increasing frequency of recent browse. We conclude that snow cover in these stands, which ranges from ca. 25 to 85 cm maximum winter depth, may offer cedar seedlings some protection from browse during winter.

The second objective was accomplished by conducting a series of chi-squared goodness-of-fit tests analyzing the abundance of eight common tree species and one shrub species against browse frequency. Results clearly showed hardwood and deciduous shrub species were selected overall, but elevated selection of cedar was seen in plots where primary use by deer was likely, and elevated *Abies balsamea* (L.) Mill selection in plots with greater regional moose densities. These results suggest that cedar regeneration in these study sites is impacted by hare and moose, but deer browse is a more likely cause of the poor recruitment of cedar seedlings and sapling.

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CHAPTER 1

MICROSITE REQUIREMENTS FOR SUCCESSFUL REGENERATION OF LOWLAND NORTHERN WHITE-CEDAR *(Thuja occidentalis* L.) FORESTS

1.1. Introduction

Persistence of productive forests relies on environmental conditions that facilitate adequate reproduction, establishment, and survival of both abundant and infrequent species. Recent studies have identified regeneration failures across a range of forest types, leading to changes in canopy species composition (Bradshaw and Waller 2016, Miller and McGill 2019). This regeneration failure may result from, or be exacerbated by, a changing climate, introduction of invasive species, changes in browsing pressure, and other changes in site conditions (Kneeshaw and Bergeron 1996, Dey et al. 2019). Regeneration failure presents challenges for management and threatens the long-term persistence of certain forest types.

Northern white-cedar (*Thuja occidentalis* L.) stands represent one such forest type. Barriers to regeneration of this species have been noted for decades (Curtis 1946, Nelson 1951) and across its geographic range (Heitzman et al. 1997, Saucier et al. 2018). While northern white-cedar (hereafter cedar) seedlings are often plentiful in cedar stands, these seedlings may exhibit mortality rates greater than co-occurring species (Curtis 1946, Larouche et al. 2011). High mortality leads to decreased cedar densities as aging cedar canopies are replaced by other tree species (Heitzman et al. 1999). Proposed causes for this regeneration barrier include increased competition, deer browsing, and unfavorable harvesting practices, yet the conditions associated with successful regeneration remain poorly understood (Heitzman et al. 1997, Larouche et al. 2010).

Despite the value of this species, cedar is thought be one of the least studied commercially important trees in this region (Boulfroy et al. 2012). Its lightweight, rot-resistant

wood comprises a specialty timber market for its use as shingles, fence posts, and other decorative outdoor applications. Additionally, cedar has long been significant to indigenous peoples for ceremonial and practical purposes (Geniusz 2015), while cedar stands provide habitat for rare plants and lichens and act as a crucial source of winter food and shelter for white-tailed deer (*Odocoileus virginianus*) (Gawler and Cutko 2010, Boulfroy et al. 2012). Yet, the poor understanding of how cedar regeneration requirements interact with site conditions represents an obstacle to effective management of this important species.

Microtopography – the fine-scale texture of the forest floor consisting of elevated mounds, depressed pits, and the flat areas in between – is thought to be vital to understanding cedar regeneration requirements, especially in swamp and seepage sites (Curtis 1946, Chimner and Hart 1996). A rough surface texture may be necessary for seed retention, allowing seeds to settle on microsites favorable to germination (Cornett et al. 1997). Microtopographic heterogeneity allows for variable soil chemistry and moisture conditions that can support a diverse plant community (Nelson 1951, Beatty 1984). A greater understanding of the influence of microtopography and related soil moisture conditions on cedar regeneration establishment and survival may be crucial in determining appropriate forest management methods.

Spatial patterning of individual stems can also shed light on regeneration dynamics and selective use of microsites, yet we know of no study involving a thorough investigation of cedar spatial patterns. The spatial arrangement of various size classes within a species can indicate the distribution of favorable conditions across a site as well as the species' fidelity to those microsites. Spatial analyses also illustrate patterns of mortality and disturbance (Kenkel 1988), and may reveal patterns of regeneration establishment of both seed and vegetative origin (Silla et al. 2002). Examining the spatial dependence between groups can also illuminate differences and

similarities in microsite associations (Poznanovic et al. 2014). Spatial association between regeneration and overstory trees has been used to assess the importance of canopy gaps in stand development (Nicotra et al. 1999, Rice et al. 2012).

We investigated the conditions associated with successful cedar regeneration (the occurrence of living seedlings or saplings) by studying fine-scale site characteristics and spatial patterning of seedlings and saplings across a range of lowland cedar stands. Fifteen stands at five sites throughout Maine, USA, were selected for study, which included detailed mapping and measuring of seedlings, saplings, and trees. Our objectives were to 1) characterize the microsite conditions associated with the occurrence of live cedar regeneration, and 2) describe how spatial patterning exhibited by cedar at different size classes relates to regeneration and recruitment outcomes. Findings from this study will benefit recent concerted efforts to identify appropriate management for this important yet poorly understood forest type (Boulfroy et al. 2012).

1.2. Methods

1.2.1. Study Sites

This work was conducted at five forested sites currently under conservation status or otherwise set aside from harvesting. These sites were located in north, central, and eastern Maine, USA and were known to include substantial cedar populations (Figure 1). Two additional sites were evaluated but excluded because they contained too few suitable cedar stands. At each of the five sites chosen, we selected three lowland cedar stands that 1) had > 65% cedar relative basal area of overstory trees with diameter at breast height (DBH, 1.4 m) ≥10 cm, 2) were large enough to accommodate a 35 × 35 m research plot, given that cedar stands in this region often occur as 'micro-stands' (*sensu* Boulfroy et al. 2012), and 3) had no recent history of harvest (cut stumps, if present, were in advanced stages of decay). These criteria were necessary to identify

stands where natural cedar regeneration dynamics could be observed. A total of 44 possible stands were visited and evaluated before selecting the 15 (three at each of five sites) used in this study. The sites and stands span a range of ownerships and represent the diversity of stand structures and apparent disturbance histories typical of Maine's cedar lowland communities (Table 12, Appendix). Many of the stands not chosen for the study were rejected because they contained only small or narrow areas of cedar-dominated overstories. This study design – three plots (representing three stands) at each site, where plots within a site are likely to be more similar to one another in climate and geography than they are to plots at other sites – was intended to allow us to consider each plot as a unique unit, while giving us the option to pool data from plots within a site to make site-level generalizations and to strengthen analyses when data sets for individual plots are insufficient. Sites include Acadia National Park (ANP), Big Reed Forest Reserve (BR), Moosehorn National Wildlife Refuge (MH), the Penobscot Experimental Forest (PEF), and Sunkhaze Meadows National Wildlife Refuge (SM). The Big Reed Forest Reserve represents old-growth (never harvested) conditions (Fraver et al. 2020); the remaining sites have been previously harvested.

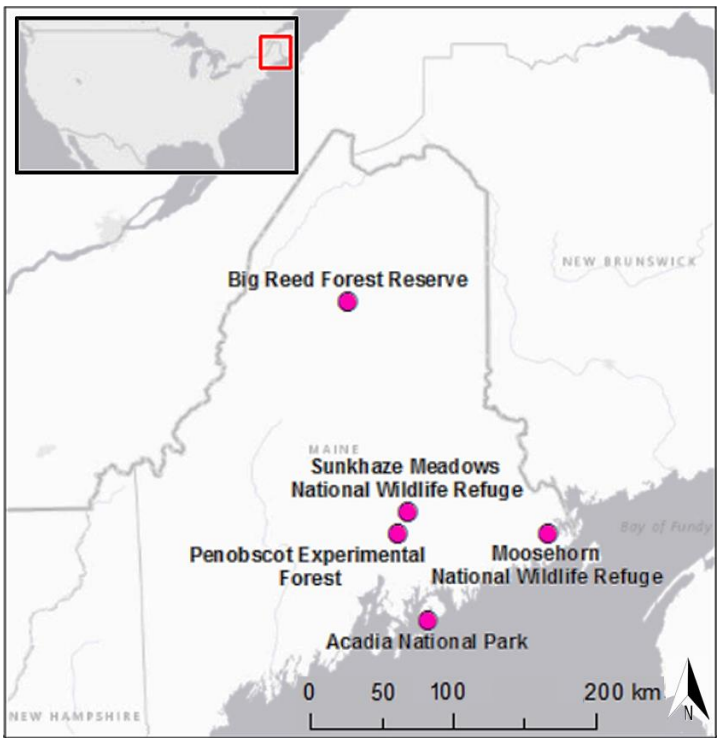

Figure 1. Site locations. Five study sites in Maine, USA.

The five study sites range in elevation from 36 m a.s.l. at ANP, located on Mount Desert Island, to 372 m a.s.l. at BR in the northern Maine highlands (U.S. Geological Survey, 2018). Annual precipitation ranges from 1073 to 1352 mm, and mean annual temperature ranges from 3.5 to 7.5°C (PRISM, 2020, 30-year normals) (Table 1). Soils are deep, poorly-drained mucky peats or decomposed plant material with lower horizons composed of loam or muck (Web Soil Survey, 2020). As is typical of this forest type, these sites have well-developed pit-and-mound (or hummock-and-hollow) microtopography (Gawler and Cutko 2010). Seasonal flooding in this forest type is common (Thompson and Sorenson 2005).

Table 1. Site locations and characteristics. Elevation data from U.S. Geologic Survey digital elevation model. Climate data based on 30-year normals from 1981 to 2010, sourced from PRISM Climate Group, Oregon State University. NWR, National Wildlife Refuge; EF, Experimental Forest.

Site	Site Abbrev.	Lat., Long.	Elevation (m)	Annual Precip. (mm)	Mean Annual Temp. (°C)
Acadia National Park	ANP	44°17' N, 68°22' W	36	1352	7.5
Big Reed Forest Reserve	BR	46°21' N, 69°03' W	372	1082	3.5
Moosehorn NWR	MH	44°51' N, 67°14' W	37	1267	6.2
Penobscot EF	PEF	44°50' N, 68°37' W	41	1073	6.4
Sunkhaze Meadows NWR	SM	44°59' N, 68°31' W	40	1098	6.4

Cedar dominated the canopy layer of all stands, with red spruce (*Picea rubens* Sarg.) and balsam fir (*Abies balsamea* (L.) Mill) also common in the canopy. Shrub communities consisted of patchy populations of several deciduous, mostly small shrubs, with sheep laurel (*Kalmia angustifolia* L.), speckled alder (*Alnus incana* (L.) Moench), and fly honeysuckle (*Lonicera canadensis* W Bartram ex Marshall), the most common species. The herbaceous understories were generally sparse and presumed largely inconsequential with regard to tree species regeneration. Nevertheless, substantial fern and graminoid communities existed at four plots. Ground cover largely consisted of bryophyte mats and litter. Details regarding plant species composition may be found in the Results section.

1.2.2. Data Collection

1.2.2.1. Plot Establishment

All plot sampling was completed between May and August of 2019. Within each of the 15 stands we established one 35 × 35 m plot (Figure 2). Plots were generally placed in the geographic center of the stands oriented such that plot borders followed cardinal directions. However, when stand shape, property boundary, or other constraints precluded such placement, plots were shifted or oriented differently to avoid these obstacles. Plot borders were demarcated

with measuring tapes. In the center of each of these full plots, we established a 15 × 15 m interior plot for more detailed inventory of seedlings, saplings, and microtopography.

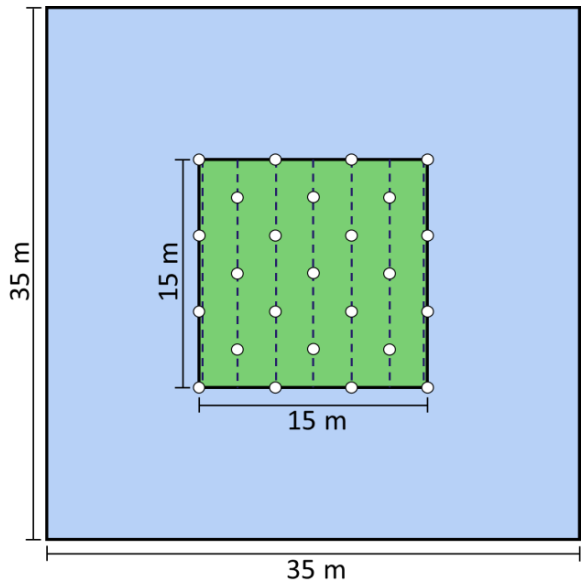

Figure 2. Plot design. A 35 × 35 m full plot and a 15 × 15 m interior plot. White points indicate locations at which hemispheric canopy photos were taken to evaluate canopy openness above the seedling layer. Dashed lines represent transects used in the microsite line-point intercept survey.

1.2.2.2. Measuring and Mapping Three Size Classes

All trees with DBH ≥ 10 cm in the full plot were inventoried, recording DBH, species, and status (live or dead). Stem centers at tree bases were mapped to the nearest decimeter as X and Y coordinates. The plot borders were used as axes wherein the southwest corner was (0, 0) and the northeast corner was (35, 35). For severely leaning trees with crowns entirely offset from the stem (not uncommon for cedar), we estimated the crown center coordinates for the purpose of producing canopy-cover maps. Crowns of trees growing straight or nearly so were considered to have the same center coordinates as the stem.

All cedar saplings (stems taller than 1.4 m and DBH <10 cm) in the full plot were mapped in the same manner as trees, recording DBH, status (live or dead), live crown ratio (LCR, an estimate of the percent of the trunk bearing live branches), presence of browse, and microtopographic feature on which the sapling was rooted. Microtopographic features were

defined as follows: mounds are raised areas on the forest floor from which water is expected to drain, pits are depressions where water would pool, and flats are level expanses or transitions between mounds and pits where water would not entirely drain or pool under typical conditions. While coarse woody debris is thought to be a favorable rooting substrate for cedar and other species (Scott and Murphy 1987), we did not categorize features by underlying material due to the difficulty in detecting decomposed woody debris without excavating and disturbing the substrate. Browse (browse observed or no browse observed) was recorded as well as apparent browser (ungulate or hare). Hare browse was identified as clean, 45° shears, and ungulate browse was identified as jagged tears, as described by Pierson and DeCalesta (2015) (Figure 10, Appendix). Only live branches within reach of deer (up to 2 m elevation) were examined for browse determinations. The same data (excluding microtopography) were collected for live saplings of non-cedar tree and shrub species in the interior plot only.

Cedar regeneration is moderately shade tolerant and often persists in a suppressed state in the understory for long periods before either senescing or being released and growing into the canopy (Ruel et al. 2014, Larouche and Ruel 2015, Fraver et al. 2020). Therefore, cedar stands may contain old, suppressed individuals still in the sapling size class, as defined above. We do not assume these older individuals representative of actively growing saplings, nor are their microsite conditions presumed to be representative of those that lead to successful recruitment. Therefore, we differentiated between ‘vigorous saplings’ and ‘suppressed sapling’ in order to exclude the latter from our analyses. In the field, all individuals in the saplings size class were inventoried, but those with poor form featuring many dead branches and low live crown ratios indicative of poor vigor were noted as likely being suppressed (Oliver and Larson 1996). To confirm that the judgements made in the field reflect predictable morphological differences, a

training subset of these data (N=632) were used in a logistic regression predicting vigorous vs. suppressed (as noted during field sampling) with DBH and LCR as independent variables (Table 13, Appendix). A cutpoint of resulting linear predictor values based on optimal sensitivity and selectivity was calculated using the 'cutpointr' R package (Thiele and Hirschfeld 2020) (Figure 11, Appendix). We then calculated the predicted values of the remaining records (validation subset) judged in the field to be vigorous or suppressed (N=632). These predicted values were used to divide the validation subset records into the two groups separated by the cutpoint. This procedure resulted in vigorous vs. suppressed determinations of the validation subset that matched the judgements made in the field for 98% of records. In this way we assessed the model's ability to differentiate between the morphological classes, where the suppressed group was characterized by low LCR compared to other individuals of the same DBH. In total, 15% of the individuals recorded in the sapling size class were suppressed; these were excluded from further analyses, leaving 1,456 true cedar saplings for analysis.

Live and dead cedar seedlings and live seedlings of other tree and shrub species were mapped (X, Y coordinates, nearest cm) and measured (height, nearest cm) in the interior plot (Figure 2). Seedlings were defined as individual stems of tree and shrub species (excluding subshrubs) between 15 and 140 cm in height. The lower limit is intended to exclude the ephemeral seedling bank, allowing us to evaluate only established seedlings. However, due to the tendency for cedar seedlings to become prostrate and root along the stem, those shorter than 15 cm were considered established and included in the survey if they produced at least three branches with scale-like (mature) foliage (adapted from Curtis 1946). Browse and microtopography were recorded as for saplings. A total of 8,331 cedar seedlings were used in analyses.

1.2.2.3. Stem-Level Metrics: Crowding and Canopy Openness

To characterize the neighborhood crowding experienced by cedar regeneration, we used the mapped locations of seedlings and saplings to estimate crowding intensity. We used the spatially explicit crowding index (CI) developed by Hegyi (1974), which incorporates both the size and proximity of neighboring stems relative to a focal stem. The CI is calculated as follows:

$$CI_f = \sum_{n=1}^{N} \left(\frac{S_n / S_f}{Distance_{nf}} \right)$$

where CI_f is the crowding index for an individual focal stem, with larger CIs indicating greater crowding; N is number of stems in a fixed-radius neighborhood around the focal stem, S_n and S_f are the size of a neighboring stem and the focal stem, respectively; and $Distance_{nf}$ is the distance between the focal stem and a neighboring stem.

Crowding indices were calculated separately for seedlings and saplings for use in analyses in which these size classes are likewise treated separately. In calculating the CIs, all live and dead cedar seedlings and saplings were used as focal stems, and all stems of woody species were used as neighbors. We used height as the CI size metric for seedlings (median height=18 cm, mean=25.3 cm) and DBH as the size metric for saplings (median DBH=1.1 cm, mean=1.4 cm).

As in previous studies based on CIs, it was necessary to determine appropriate neighborhood radii for seedlings and saplings. We followed the recommendation of Lorimer (1983), which establishes the radius as 3.5 × the mean crown radius of the focal species. For seedlings, this neighborhood radius was 0.21 m, that is, 3.5 × the median seedling crown radius of 0.06 m, based on 306 cedar seedling crowns measured for this purpose at three sites. We used

median instead of mean crown radii, given the skew toward the smaller crown sizes. These measured seedlings were selected in a stratified manner to reflect the height distribution of the entire cedar seedling data set. Saplings may have occurred within the neighborhood radius of seedlings but were not included in the index; however, their influence was captured by the canopy openness values derived from hemispherical photographs (see below). For saplings, the neighborhood radius was 2.1 m, that is, 3.5 × the median cedar sapling crown radius of 0.59 m (Fraver, unpublished data). CIs for focal stems located within 0.21 m (seedlings) or 2.1 m (saplings) of the plot border required edge correction. For these, the CIs were adjusted upward according to the proportion of their neighborhood that fell outside the plot (following Haase 1995).

To characterize canopy openness experienced by seedlings, we used hemispheric photos taken on a regular grid through the interior plot. Thus, 25 canopy photos were taken from a height of 140 cm, along parallel transects separated by 2.5 m (Figure 2). Additionally, canopy photos were taken above all dead cedar saplings and a subset of live cedar saplings. The subset of live saplings included all those in the interior plot plus additional saplings from the full plot as needed to obtain at least 20 saplings total. Photos were taken above all saplings in plots with fewer than 20 saplings. Sapling photos were taken directly above the sapling using a camera (with gimbal mount) attached to a telescoping pole. For tight clusters of saplings all of similar height, one photo was taken for the cluster. We used a Kodak PixPro camera with a fish-eye lens set in a Regent Instruments (Ste-Foy, Quebec, Canada) Mini-OMount system.

Hemispheric photos were processed using Gap Light Analyzer software (Frazer et al. 1999) to obtain canopy openness, excluding outer rings beyond a 60° zenith angle. Canopy openness values for cedar saplings were derived directly from the hemispherical photos taken

above individual saplings or tight clusters of saplings. Seedling canopy openness was interpolated by applying kriging to the 25 grid photos taken in each interior plot. Kriged surfaces were created using ordinary kriging based on spherical (or best fit) models using the 'gstat' R package (Gräler et al. 2016). Kriging produced a grid of one-meter-square cells, the values of which were extracted and applied to all seedlings located in that cell.

1.2.2.4. Microtopography and Plot-Level Metrics

To examine the relationship between microtopography cedar regeneration abundance it was necessary to quantify the proportions of each plot occupied by the three microtopographic features. We used a line-point intercept survey along seven equally spaced, 15-m-long transects running north-south through the interior plot to obtain percent occurrence of each feature. An observation was made every 0.5 m along each transect (N=217 per plot), and microtopographic feature was recorded. Furthermore, to link microtopographic feature to relative soil moisture, a single series of volumetric water content readings were taken on a random selection of 25 mounds, 25 flats, and 25 pits, using a Fieldscout TDR 150 (Spectrum Technologies, Inc.) fitted with 7.5 cm prongs. These measurements were taken between May 31 and August 27. Features were selected subjectively following no regular pattern to ensure that a representative sample of each feature was obtained across the interior plot. This survey was never conducted during rain or within 24 hours after a rain event, and all measurements in a plot were made within 30 minutes of each other. These measurements are intended to reflect relative soil moisture of the three features at that point in time, regardless of absolute moisture content or differences in soil conditions between plots.

To augment the structural descriptions of these stands, we inventoried downed coarse woody debris (CWD) using the line intersect method (Van Wagner 1968) applied to two 49.5-m

transects arranged diagonally between plot corners. This length produces an acceptable level of precision for this forest type (Fraver et al. 2018). For each CWD piece ≥ 10 cm diameter intersected by the sampling transect, we recorded diameter at intersection, species (when not precluded by advanced decay), and decay class (five-class system of Sollins 1982). Woody debris volumes per hectare were determined as per Van Wagner (1968). To account for the gradual collapse through decay, volumes of advanced decay pieces were reduced using reduction factors of 0.800 and 0.412 (classes 4 and 5, respectively; Fraver et al. 2013).

1.2.3. Analyses

1.2.3.1. Soil Moisture

We tested the relationship between relative soil moisture and microtopographic feature to explore how variations in observed soil moisture among the features might influence establishment and recruitment of seedlings and saplings. Volumetric water content values were converted to z-scores within each plot. We developed a linear mixed-effects model to test if z-scores varied by microtopographic feature, treating features as fixed variables and plots-within-sites as a random variable. The 'EMSaov' R package (Choe et al. 2017) was used to develop the model and produce the resulting ANOVA table. Tukey's tests were then used as *post-hoc* analyses of the model results to assess moisture differences among microtopographic features at a significance level of 0.05.

1.2.3.2. Occurrence by Microtopographic Feature

To determine if cedar regeneration is likely to have a stronger association with certain microtopographic features, we used chi-squarred goodness-of-fit tests. The numbers of live cedar seedlings found on mounds, flats, and pits were compared to the proportion of each of those features as determined by the line-point intercept surveys. *P*-values were calculated for the

residuals of each cell to determine if there were more or fewer seedlings than expected given the frequency of features on the plot. Given the low numbers of seedlings on particular features at several plots, we pooled plots (within sites) and conducted these analyses at the site level to demonstrate patterns across the study area. We conducted an additional analysis using averages of all sites combined to assess the strength of the patterns overall. The same test procedure was applied to live cedar saplings. The PEF site was excluded because it did not contain a sufficient number of saplings ($N \geq 20$).

1.2.3.3. Modeling Regeneration Status and Vigor

To explore the likely relationships between microsite conditions and the success (occurrence of live individuals) of cedar regeneration, we created and evaluated two logistic mixed-effects regression models – one for saplings and one for seedlings – in which status (live or dead) served as the response variable. In addition, for saplings, we evaluated a mixed-effects regression model with LCR as the response variable. We used LCR as a measure of vigor, with greater ratios indicating enhanced vigor (Daniels and Burkhart 1975, Berrill and Dagley 2012). Combinations of microsite conditions were treated as the fixed effects, and site was included as a random effect. Because we had too few observations for certain response variables (canopy openness among saplings and certain microtopographic features for both size classes) at the plot level, plots within site were pooled. These analyses were conducted with the 'lme4' R package (Bates et al. 2015). All candidate models within each of the three analyses were ranked by the Akaike information criterion (AIC) and conditional R-squared values.

The first set of models tested seedling status (live or dead) as the response variable in a generalized logistic mixed-effects model using crowding index, canopy openness, microtopographic feature on which the seedling is rooted, the interaction between canopy

openness and microtopographic feature, and browse (browsed or not browsed) as fixed predictors. Models were created with every possible combination of these variables. Seedling height was not included because a large portion of dead seedlings were browsed or otherwise broken, preventing a reliable determination of height at the time of death.

The second set of models tested sapling status (live or dead) as the response variable in a generalized logistic mixed-effects model, using DBH, crowding, canopy openness, microtopographic feature, and the interaction between canopy openness and microtopographic feature as fixed predictor variables. These same variables were used in the third set of models that tested sapling LCR as a response variable in a mixed-effects regression model. In both sets of sapling models, each variable was tested individually and in all possible combinations, with the exception of DBH which was present in all models, given the well-documented importance of size for growth (Enquist et al. 1999) and survival (Coomes and Allen 2007). Browse was not included because many larger saplings had no live branches within reach of browsers, and this would likely result in a biased sample. We included only those saplings (N=412) for which we derived canopy openness values from hemispheric photographs. The PEF site was excluded from both analyses due to small total numbers of saplings, and the SM site was also excluded from the status analysis due to a small number of dead saplings.

1.2.3.4. Assessing Spatial Dependence

We began our spatial analysis by depicting patterns using stem maps created using the 'ggplot2' R package (Wickham 2016). Four series of stem maps were created to illustrate patterns within and among species. The first series shows the locations of seedlings plotted on the resulting canopy openness kriged surfaces. The second series shows the locations of live cedar seedlings in the interior plot in relation to the crowns of all live trees and saplings. The

third series illustrates the locations of live cedar saplings with the crowns of all live trees. Though cedar saplings were mapped throughout the full plot, the outermost 5 meters of the plot were excluded from these maps due to the possibility of crowns of trees rooted outside extending over the full plot. The fourth series of maps included all live trees scaled by DBH. To create the second and third series of maps, we estimated the circular crown projection areas for each tree and sapling based on its DBH, using species-specific equations (Fraver, unpublished data, see Table 14, Appendix) based on stem-center-to-dripline measurements in four cardinal directions, and with projection area calculated as the sum of the resulting four quarter ellipses (Frelich and Lorimer 1991).

The detailed stem-mapped data allowed us to conduct a number of spatial pattern analyses that could shed light on factors influencing successful establishment of seedlings and recruitment of saplings. We used the univariate *L(t)* transformation of Ripley's *K(t)* function (Ripley 1977) to analyze the spatial patterns of live cedar trees, saplings, and seedlings. Point-pattern datasets were created containing the X and Y coordinates for individuals within each of the three size classes at each plot. Datasets with fewer than 20 individuals were considered insufficient for analysis and were excluded. We created graphical envelopes of simulated values representing a predicted interval of complete spatial independence at a significance level of 0.05, using the 'spatstat' R package (Baddeley et al. 2015). The envelope was based on 39 Monte Carlo simulations to achieve a significance level of 0.05, as determined by the software. Simulation envelopes were plotted along with the observed spatial data to visually assess deviations from the null hypothesis of spatial randomness across distances up to half the length of a plot side (17 m for saplings and trees, 7.5 m for seedlings).

We then used the bivariate *L(t)* function to test the spatial independence of cedar seedlings and saplings, and between those groups and the overstory. The former analysis was intended to determine differences or similarities regarding microsite use between size classes, and the latter two analyses test if regeneration tended to occurred away from overstory cover. Marked point pattern datasets were created including the X and Y coordinates of the groups being compared. Datasets in which one or both groups contained fewer than 20 individuals were excluded from analysis. These datasets were used to generate simulation envelopes and to plot the observed spatial data following the procedure used for the univariate *L(t)* analyses. We analyzed the results for evidence of attraction or repulsion against the null hypothesis of independence.

1.3. Results

1.3.1. Stand Structure and Composition

Stand structural metrics varied widely among plots, with each plot representing a unique stand (Table 2). In general, the Big Reed plots had the highest live-tree basal areas and lowest live-tree tree densities (means 56.7 m^2 ha^{-1}, 765 trees ha^{-1}, respectively), while the Acadia National Park plots had the lowest basal areas (mean 40.8 m^2 ha^{-1}), and the Penobscot Experimental Forest had the highest tree densities (mean 1665 trees ha^{-1}). Volumes of coarse woody debris also varied widely among plots, ranging from 24.5 m^3 ha^{-1} (ANP2) to 219.1 m^3 ha^{-1} (BR3). Table 2 provides structural details for all plots, and Table 15 (Appendix) presents relative basal areas of all tree species, all plots.

Table 2. Stand summary metrics. Plot are organized by site, alphabetically. BA, basal area; NWR, National Wildlife Refuge.

Site Plot	BA (m2 ha^{-1})	Stems (trees ha^{-1})	DBH (cm) mean (SD)	Cedar rel. BA (%)	CWD vol. (m3 ha^{-1})
Acadia National Park					
ANP1	41.5	1282	19.6 (5.2)	85.9	32.0
ANP2	50.0	1486	19.5 (6.9)	88.7	24.5
ANP3	30.8	727	21.9 (7.8)	78.9	61.8
Big Reed Forest Reserve					
BR1	58.6	686	28.3 (17.0)	91.8	127.0
BR2	62.8	857	26.7 (14.9)	93.9	116.2
BR3	48.8	751	25.6 (13.1)	81.1	219.1
Moosehorn NWR					
MH1	61.3	971	26.9 (9.0)	86.8	64.6
MH2	42.4	1078	21.2 (7.4)	92.3	64.1
MH3	47.2	1004	22.7 (9.2)	68.9	50.7
Penobscot Experimental Forest					
PEF1	62.8	1951	19.5 (5.5)	93.4	45.8
PEF2	52.5	1641	19.0 (6.7)	68.1	27.5
PEF3	38.4	1404	17.8 (5.5)	67.0	47.0
Sunkhaze Meadows NWR					
SM1	39.6	873	22.3 (9.0)	82.1	46.8
SM2	44.6	1176	20.7 (7.2)	85.3	39.3
SM3	62.8	1306	23.3 (8.3)	78.0	37.3

The relative basal area of cedar ranged from 67% at plot PEF3 to 94% at plot BR2. In addition to cedar, red spruce and balsam fir were common canopy species at all sites. Red maple (*Acer rubrum* L.), black ash (*Fraxinus nigra* Marshall), eastern hemlock (*Tsuga canadensis* (L.) Carrière), paper birch (*Betula papyrifera* Marshall), yellow birch (*B. alleghaniensis* Britton), and tamarack (*Larix laricina* (Du Roi) K. Koch) were also present in smaller numbers (Table 15, Appendix). Common tree and shrub species accompanying cedar in the understory (sapling and seedling layers) include balsam fir, red maple, red spruce, speckled alder, tamarack, black ash, yellow birch, sheep laurel, fly honeysuckle, eastern hemlock, huckleberry (*Gaylussacia baccata* (Wangenh.) K. Koch), mountain holly (*Ilex mucronata* (L.) Powell, Savolainen & Andrews), and

winterberry holly (*I. verticillata* (L.) A. Gray), listed in decreasing abundance, stands pooled (Table 16 and Table 17, Appendix).

Understory herbaceous communities also varied among plots. Considerable fern cover was present at plots ANP2, ANP3, PEF2, and PEF3 featured, ranging from approximately 10% to 45% cover. Fern cover at ANP2 was almost exclusively cinnamon fern (*Osmunda cinnamomea* L.), while the communities at the other three plots were more diverse, including sensitive fern (*Onoclea sensibilis* L.), royal fern (*Osmunda regalis* L.), and marsh fern (*Thelypteris palustris* Schott). Additionally, graminoids accounted for about 10-35% cover at plots ANP2, ANP3, and PEF3. The graminoid communities were largely composed of two or more sedge (Cyperaceae) species. ANP3 and PEF3 exhibited the largest overall percent of fern and graminoid cover.

Species in the genus *Sphagnum* L. as well as *Hylocomium splendens* (Hedw.) Schimp. and *Bazzania trilobata* (L.) A. Gray were well-represented at all sites and were dominant components of the ground-cover bryophyte communities at a majority of plots. All three ANP plots, in particular, were dominated by *Sphagnum* species. *Rhytidiadelphus triquetrus* (Hedw.) Warnst. was also common in the pits and wetter flats at a majority of plots, but was not a major ground cover at the ANP plots. Most plots featured *B. trilobata* commonly on raised dead wood features (stumps and logs in early stages of decay). *Thuidium delicatulum* (Hedw.) Schimp and *Pleurozium schreberi* (Brid.) Mitt were each common at a minority of plots, particularly plots at the MH and PEF sites, where they were often found on mounds and drier flats. *Trichocolea tomentella* (Ehrh.) Dumort was often found in pits at BR and PEF plots. Other mosses prominent

at individual plots were *Calliergon cordifolium* (Hedw.) Kindb, *Fissidens* sp. Hedw., *Hypnum lindbergii* Mitt, *Rhizomnium pseudopunctatum* Bruch & Schimp.) T. Kop., and *R. punctatum* (Hedw.) T. Kop.

1.3.2. Soil Moisture

Our mixed-effects model results indicated that microtopographic feature is a strong predictor of relative soil moisture measured between May 31 and August 27, with mean moisture decreasing in the order pits > flats > mounds. The Tukey's *post-hoc* test demonstrated that the pair-wise differences between mean moisture for the three features were significant ($P < 0.05$) (Figure 3). Additionally, the interaction between feature and plot-within-site was significant ($P < 0.05$). The interaction between feature and site was only slightly below the chosen threshold of significance ($P = 0.04$). (Table 3). These interactions indicated that soil moisture differences between features varied by plot (e.g. soil moisture on flats was more similar to mounds at some plots and more similar to pits at others). Despite these differences, every plot demonstrated the same pattern regarding moisture: pits were wetter than flats, and flats were wetter than mounds (Figure 12, Appendix).

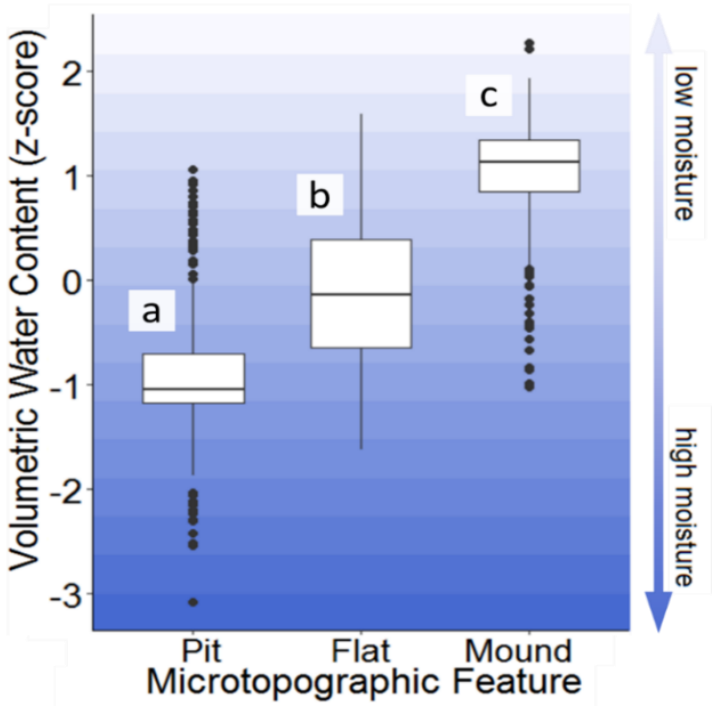

Figure 3. Soil moisture by microtopographic feature. Distribution of volumetric water content values (z-scores) recorded on three microtopographic features (N=375 for each feature). For visual interpretation z-score values were inverted such that greater moisture readings are negative and lower moisture readings are positive. Letters indicate results of Tukey's *post-hoc* test where different letters are assigned to different means ($P < 0.01$).

Table 3. Soil moisture model results. Results of a mixed-effects model predicting relative soil moisture (z-scores of volumetric water content) from microtopographic feature. Plot-within-site is used as a random effect, and two interactions are included. Microtopographic feature is shown to be a strong predictor of relative soil moisture. df, degrees of freedom.

Variable	**df**	***F*-value**	***P*-value**
Site	4	0.48	0.75
Plot (Site)	10	0.00	1.00
Feature	2	197.73	<0.001
Site × Feature	8	2.57	0.04
Plot × Feature (Site)	20	2.04	0.005
Residuals	1080		

1.3.3. Occurrence by Microtopographic Feature

All sites were dominated by flats. Pits were the least abundant feature at all sites except PEF, which had a smaller proportion of mounds. The chi-squared goodness-of-fit tests showed the observed numbers of seedlings on mounds to be significantly greater than expected based on

mound prevalence, and significantly fewer seedlings than expected were found on flats and pits (Figure 4a). This finding held for all microtopographic features at most sites, with flats at the PEF being the only exception. The same general trend was observed among saplings; however, the relationship was not as pronounced. In fact, the SM site revealed no differences between observed and expected sapling numbers across features (Figure 4b).

a. Seedlings

Site / Feature	Acadia National Park	Big Reed Forest Reserve	Moosehorn NWR	Penobscot EF	Sunkhaze Meadows NWR	All Sites
Mounds	2003 (36.5)	736 (5.1)	525 (17.5)	46 (2.5)	421 (6.1)	746 (17.5)
Flats	1535 (-27.9)	1234 (-2.6)	396 (-14.4)	93 (0.1)	636 (-2.7)	779 (-10.0)
Pits	148 (-10.2)	162 (-3.5)	39 (-3.9)	33 (-2.4)	76 (-4.7)	92 (-8.6)

b. Saplings

Site / Feature	Acadia National Park	Big Reed Forest Reserve	Moosehorn NWR	Sunkhaze Meadows NWR	All Sites
Mounds	150 (9.9)	231 (3.4)	152 (2.9)	36 (0.4)	142 (3.7)
Flats	65 (-8.0)	372 (-1.8)	231 (-1.4)	55 (-1.1)	181 (-2.1)
Pits	20 (-2.1)	46 (-2.3)	20 (-2.3)	15 (1.1)	25 (-2.2)

Figure 4. Regeneration occurrence by microtopographic feature. Heat maps displaying results of chi-squared goodness-of-fit tests comparing numbers of cedar seedlings (a) and saplings (b) with the proportions of three microtopographic features. Average frequencies across sites were also analyzed to highlight general trends. Numbers of stems present are displayed followed by the residual of the chi-squared test. Green diagonal shading indicates more stems than expected, and orange cross-hatched shading indicates fewer stems than expected ($P \leq 0.05$). Intensity of colors corresponds to magnitude of the deviation from expected frequencies (residual values), where unshaded cells do not significantly differ from expectations (residual close to zero such that $P \geq 0.05$). NWR, National Wildlife Refuge; EF, Experimental Forest.

1.3.4. Modeling Regeneration Status and Vigor

The six predictor variables used in the seedling status (live or dead) logistic regression (five variables plus one interaction) arranged in all possible combinations yielded twenty models for evaluation. A ΔAIC threshold of 10 was chosen to classify high-ranking models in this analysis and the following regression analyses based on a natural break observed in the results (Burnham and Anderson 2003) (Table 4a). Variables were assessed using *P*-values of less than 0.05 or 0.157, the latter reflecting the significance levels typically seen among variables in AIC-selected models (Heinze et al. 2018). Six of the twenty seedling status models were considered high-ranking. Browse and microtopography were present in all the high-ranking models. Browse and pits were generally associated with dead seedlings, while mounds and flats were generally associated with live seedlings. Canopy openness appeared in four top models and was positively associated with status (live seedlings were more likely to occur under greater canopy openness). Crowding and the interaction term appeared in three and two top models, respectively, but were not significant predictors on their own.

All possible combinations of predictor variables in the sapling status (live or dead) logistic regression yielded 10 models, three of which were considered high-ranking with ΔAIC less than 10 (Table 4b). DBH was included in all models analyzed showing a negative association with status (larger saplings were more likely to be dead), but the effect was not significant. All predictor variables were included in at least one high-ranking model. Canopy openness appeared as a strong predictor in all three high-ranking models where greater openness was associated with live saplings. Microtopography (mounds and flats only, as there were too few dead saplings found in pits for analysis) appeared in two models and was a significant predictor in one of these, where flats were more associated with live saplings than were mounds.

While the interaction term was not significant on its own, it appeared in one top model showing a better fit than some other, more parsimonious models. Crowding appeared in all three models and was positively associated with status (saplings in more crowded environments were more likely to be alive). Note that the crowding index characterized the sapling neighborhood, while canopy openness accounted for the overstory, such that these two variables are not directly related.

All possible combinations of predictor variables in the sapling LCR linear regression yielded ten models for evaluation, and two of these were considered high-ranking (Table 4c). DBH was consistently negatively associated with LCR. Canopy openness was present in both high-ranking models, showing a strong positive association with LCR. Crowding appeared in one top model with a negative association (i.e., crowded saplings had lower LCRs). Neither microtopography nor the interaction were present in the top models.

Table 4. Regeneration status and vigor model summaries. High-ranking status (live or dead) and live crown ratio (LCR, a measure of vigor expressed as natural log) models are shown. Mixed-effects logistic regressions with seedling (a) and sapling (b) status as the response variable, and a mixed-effects linear regression with sapling LCR as a response variable (c). Fixed predictor variables represent stem-level environmental characteristics. Site was included as a random effect. Models with ΔAIC >10 were considered low-ranking are not shown. Model estimates are presented, with positive results representing an association with live status or high LCR, and negative results representing an association with dead status or low LCR. Brws., browse; Y, browse observed; N, no browse observed; CI, natural log of crowding index; CO, natural log of canopy openness; Micro., microtopographic feature; M, mounds; F, flats; P, pits; dbh, natural log of stem diameter; k, number of model parameters; AIC, Akaike information criterion; R^2, conditional R^2; * $P < 0.157$; ** $P < 0.05$.

a. Seedling Status

	Brws.				Microtopography			CO • Microtopography						
Model (Live/Dead =)	Y	N	CI	CO	M	F	P	CO • M	CO • F	CO • P	k	AIC	ΔAIC	R^2
Brws. + CO + Micro.	-	1.76**		5.30**	-	0.14	-0.76**				6	1944.2	0.00	0.20
Brws. + CI + CO + Micro.	-	1.74**	0.04	0.69**	-	0.13	-0.75**				7	1945.4	1.22	0.20
Brws. + Micro.	-	1.76**			-	0.14	-0.75**				5	1947.5	3.34	0.24
Brws. + CO + Micro. + (CO • Micro.)	-	1.76**		0.69*	-	0.17	-0.48	-	0.02	0.13	8	1948.1	3.95	0.22
Brws. + CI + Micro.	-	1.74**	0.05		-	0.14	-0.73**				6	1948.3	4.16	0.23
Brws. + CI + CO + Micro. + (CO • Micro.)	-	1.74**	0.04	0.67*	-	0.14	-0.49	-	0.00	0.12	9	1949.3	5.17	0.22

b. Sapling Status

				Microtopography		CO • Microtopography					
Model (Live/Dead = dbh +)	dbh	CI	CO	M	F	CO • M	CO • F	k	AIC	ΔAIC	R^2
CI + CO + Micro.	-0.02	0.74**	2.32**	-	0.82**			6	218.5	0	0.43
CI + CO + Micro. + (CO • Micro.)	-0.02	0.74**	2.45**	-	1.74	-	-0.45	7	220.4	1.95	0.42
CI + CO	-0.07	0.65**	2.57**					5	221.3	2.77	0.45

c. Sapling LCR

				Microtopography			CO • Microtopography						
Model (LCR = dbh +)	dbh	CI	CO	M	F	P	CO • M	CO • F	CO • P	k	AIC	ΔAIC	R^2
CI + CO	-0.10**	-0.09**	0.61**							6	504.7	0.00	0.45
CO	-0.06**		0.51**							5	508.4	3.70	0.36

1.3.5. Stand-level Analyses

Although our analyses were intended to focus on individual stems (as above), we conducted analyses at the plot level to assess general trends. First, we found significant negative correlations between tree density and both seedling and sapling abundance ($R^2 = 0.26, 0.47$, respectively, P values ≤ 0.05). Second, we found a significant positive correlation between CWD volume and sapling abundance ($R^2 = 0.35$, P value = 0.02).

1.3.6. Assessing Spatial Dependence

Clustering was evident in the seedling stem maps of all plots. Four maps of each of the two seedling stem map series are featured in Figure 5, showing clustering that was consistent across plots, though varying in intensity. This observation was confirmed by the univariate *L(t)* function results, which demonstrated clustering of seedlings at all plots (Table 5), particularly at shorter distances. Similar results were seen among saplings at the eight plots with numbers sufficient for analysis. Four of these eight sapling maps are presented in Figure 6, and these are representative of the range of clustering observed. The univariate *L(t)* function results, again, confirmed these observations, showing saplings clustering at all distances for all plots analyzed (Table 5). Stem maps showing the locations of cedar trees and other tree species at each plot are shown in Figure 13 (Appendix). The univariate *L(t)* function results show clustering among trees at nine plots, while the remaining six plots demonstrate uniform, random, or both random and clustered arrangements (Table 5).

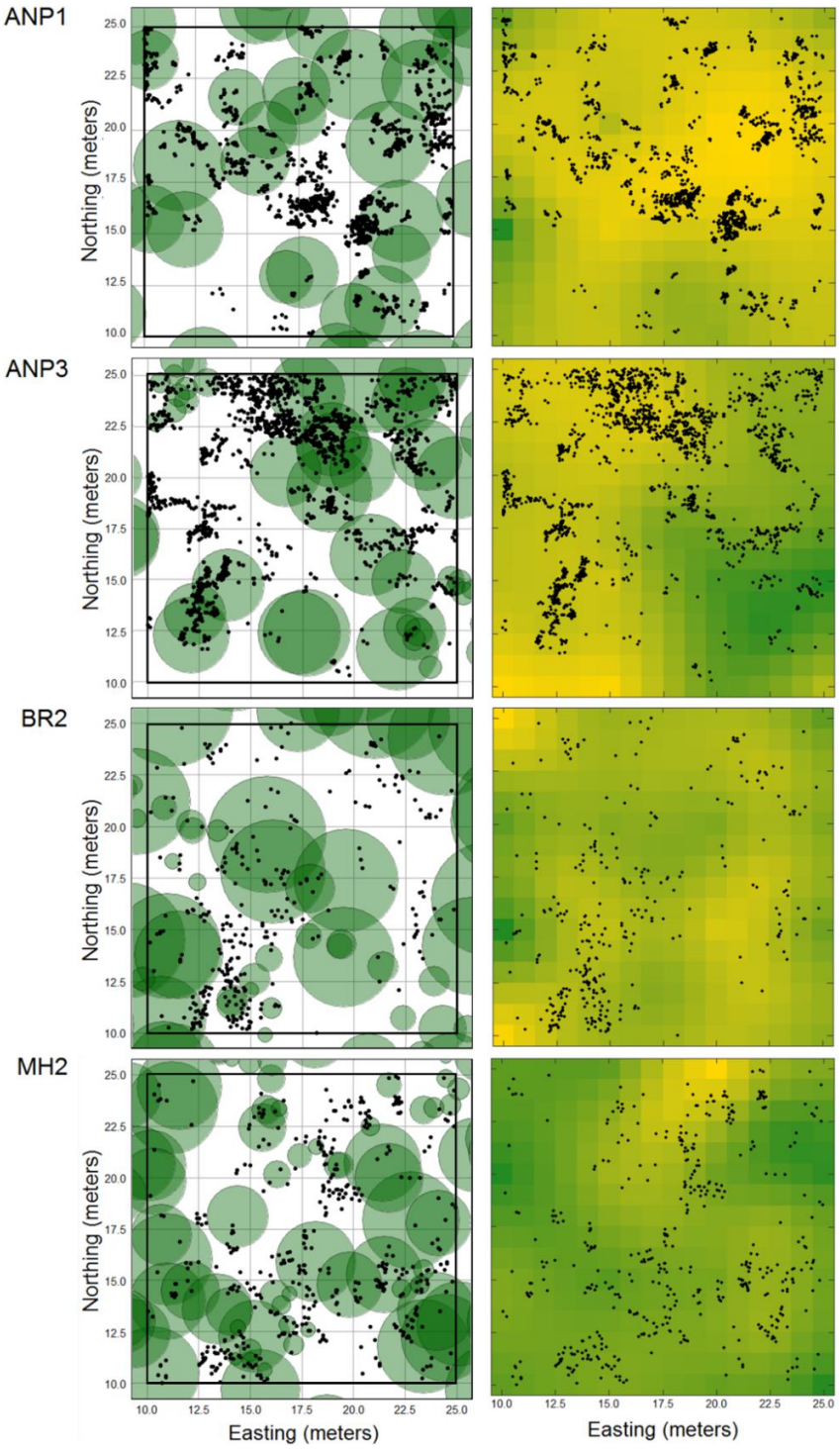

Figure 5. Seedling stem maps. Representative stem maps, selected to display a range of conditions, showing live cedar seedlings in black. On the left, seedlings are displayed in relation to live tree and sapling crown projection areas. On the right, seedlings are displayed atop a kriged surface illustrating canopy openness. Darker green indicates greater canopy cover; lighter yellow indicates more open canopy. These maps demonstrate that seedlings are clearly clustered, but are not necessarily clustered under canopy gaps.

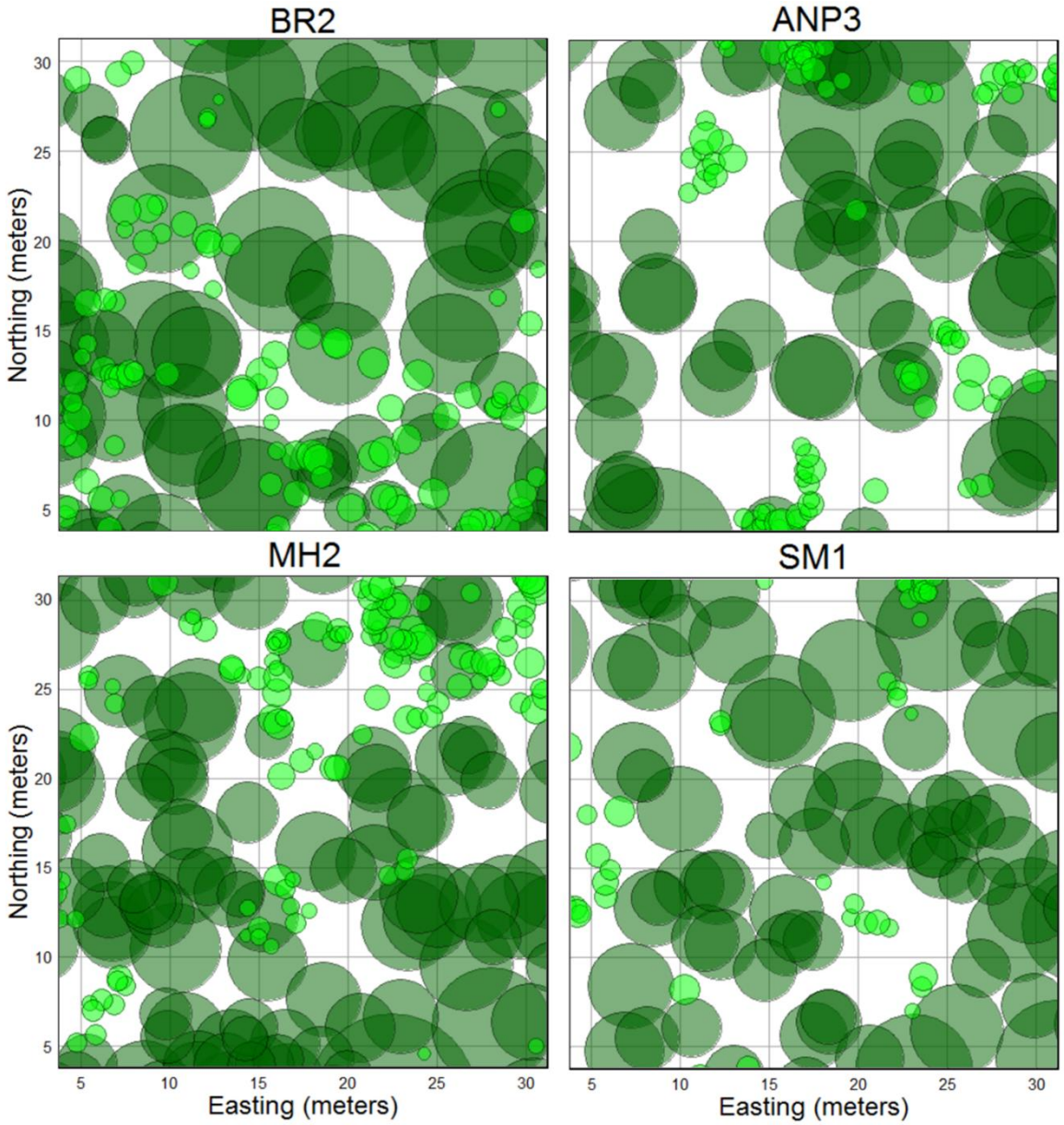

Figure 6. Sapling stem maps. Representative stem maps, selected to display a range of conditions, showing size and location of live cedar sapling crowns (light green) and all live tree crowns (dark green). All crowns are scaled by crown projection area. A 5-meter exterior buffer was excluded due to uncertainty regarding crowns of trees rooted outside the plot whose canopies may have extended into the plot. These maps illustrate the clustering pattern of saplings, as well as the variable relationship of saplings to gaps. The saplings at BR2 grew under sparse to dense canopy. Plots ANP3 and MH2 show a range of gap sizes and variable associations between saplings and gaps. Unlike BR2, saplings at SM1 were strongly associated with gaps or sparse canopy.

The four series of maps presented here (Figures 5 and 6, and Figure 13 in the Appendix) also show that most stands feature small canopy gaps likely resulting from windthrow (a common disturbance in this forest type), but cedar regeneration is only weakly associated with these gaps. The seedling maps in Figure 5 demonstrate the tendency for seedlings to occur under both low and high canopy openness without a discernable association with gaps. Likewise, the bivariate *L(t)* function results show little evidence of attraction or repulsion between cedar seedlings and cedar trees; however, we found evidence for attraction between cedar seedlings and all live trees and saplings combined, with one plot (BR1) showing clear attraction up to ca. 5 m distance (Table 6). Overall, we found a trend toward attraction between live cedar seedlings and live cedar saplings. Saplings exhibited a range of associations with gaps and denser canopy, as illustrated by the plots featured in Figure 6. For example, plot BR2 shows an especially dense canopy with few gaps for saplings to occupy. In contrast, plot SM1 shows larger gaps occupied by saplings, though this plot also had a dense population of fir saplings (not shown) that occupied much of the space under gaps. The bivariate *L(t)* function results suggested repulsion between cedar saplings and cedar trees at six sites, as would be expected if saplings grow away from the shade directly under a canopy tree, although two plots showed no relationship between saplings and trees (Table 6).

Table 5. Univariate *L(t)* function results. The univariate *L(t)* function was applied to three cedar size classes at 15 plots (results for plots containing ≥ 20 stems presented). For seedlings, patterns were analyzed every half meter from 0 to 7.5 m (half the length of the interior plot). For saplings and trees, patterns were analyzed every meter from 0 to 17 m (half the length of the full plot). Live cedar seedlings and saplings are strongly clustered at all plots. Most plots show some clustering among live cedar trees, but the trend is much weaker than those seen in the smaller size classes. C, clustered; U, uniform; '-', random.

			Distance (meters)														
	Plot	N	0.5	1	1.5	2	2.5	3	3.5	4	4.5	5	5.5	6	6.5	7	7.5
Cedar	ANP1	1668	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
Seedlings	ANP2	254	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
	ANP3	1764	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
	BR1	958	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
	BR2	289	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
	BR3	885	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
	MH1	142	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
	MH2	440	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
	MH3	378	C	C	C	C	C	C	C	C	C	C	C	-	U	U	U
	PEF1	28	C	C	C	C	C	C	-	-	-	-	-	-	-	-	-
	PEF2	77	C	C	C	C	C	C	C	C	-	-	-	C	C	C	C
	PEF3	67	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
	SM1	543	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
	SM2	419	C	C	C	C	C	C	C	C	C	C	C	C	C	-	-
	SM3	172	C	C	C	C	C	C	C	C	C	C	C	-	U	U	U

			Distance (meters)																
	Plot	N	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Cedar	ANP3	231	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
Saplings	BR1	207	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
	BR2	214	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
	BR3	228	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
	MH2	186	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
	MH3	207	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
	SM1	50	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
	SM2	51	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
Cedar	ANP1	138	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trees	ANP2	163	-	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
	ANP3	77	-	C	-	-	C	C	C	C	C	C	C	C	C	C	C	C	-
	BR1	51	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	BR2	88	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	BR3	45	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	MH1	99	C	C	C	-	C	-	C	-	-	-	-	-	-	-	-	-	-
	MH2	116	-	-	C	C	C	C	-	-	-	-	-	C	C	C	C	C	C
	MH3	87	-	C	-	-	-	-	-	-	-	-	-	-	-	-	-	U	U
	PEF1	221	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	PEF2	128	-	-	-	C	C	C	C	C	C	-	-	-	-	-	-	-	-
	PEF3	129	-	-	-	-	-	-	-	-	U	U	U	U	U	U	U	-	-
	SM1	94	-	C	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	SM2	125	-	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
	SM3	127	-	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

N, number of stems per plot; ANP, Acadia National Park; BR, Big Reed Forest Reserve; MH, Moosehorn National Wildlife Refuge; PEF, Penobscot Experimental Forest; SM, Sunkhaze Meadows National Wildlife Refuge.

Table 6. Bivariate *L(t)* function results. The bivariate *L(t)* function was used to analyze the spatial relationships between three cedar size classes, and between cedar seedlings and larger size classes of all species (results for plots containing ≥ 20 stems presented). Patterns between saplings and trees were analyzed every meter for half the length of the full plot. For relationships involving seedlings, patterns were analyzed every half meter for half the length of the interior plot. Seedlings and saplings were generally repelled by or independent of cedar trees. There was some attraction between seedlings and larger size classes of all species, and seedlings were largely attracting with saplings. R, repelling; A, attracting; '-', independent (no relationship).

		N	N	Distance (meters)																
	Plot	sapl	trees	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Cedar	ANP3	231	77	-	-	-	R	R	R	R	-	-	-	-	-	-	-	-	-	-
Saplings	BR1	207	51	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
vs	BR2	214	88	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cedar	BR3	228	45	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trees	MH2	186	116	R	R	R	-	-	R	R	R	R	-	-	-	-	-	-	-	-
	MH3	207	87	-	R	R	R	R	R	-	-	-	-	-	-	-	-	-	-	-
	SM1	50	94	-	-	R	R	R	R	R	R	-	-	-	-	-	-	-	-	-
	SM2	51	125	-	-	-	-	R	R	-	-	-	-	-	-	-	-	-	-	-

		N	N	Distance (meters)														
	Plot	seed	sapl	0.5	1	1.5	2	2.5	3	3.5	4	4.5	5	5.5	6	6.5	7	7.5
Cedar Seed.	BR1	958	42	A	A	A	A	A	A	A	A	A	A	-	-	-	-	-
vs Cedar	BR3	885	22	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-
Saplings	MH2	440	30	A	A	A	A	A	A	A	-	-	-	-	-	-	-	-
	MH3	378	22	A	A	A	A	A	A	A	A	A						
		seed	trees															
Cedar	ANP2	254	32	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Seedlings	ANP3	1764	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
vs	MH1	142	25	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cedar Trees	MH2	440	23	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	PEF1	28	40	-	-	-	-	-	-	-	-	-	-	R	R	R	-	-
	PEF2	77	22	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	PEF3	67	22	-	-	-	-	-	R	R	-	-	-	-	-	-	-	-
	SM1	543	22	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	SM2	419	21	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	SM3	172	25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		seed	T+S															
Cedar	ANP1	1668	26	-	-	-	-	-	R	-	-	-	-	-	-	-	-	-
Seedlings	ANP2	254	42	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
vs	ANP3	1764	53	A	A	-	-	A	A	-	-	-	-	-	-	-	-	-
All Trees	BR1	958	152	A	A	A	A	A	A	A	A	A	A	A	-	-	-	-
and	BR2	289	49	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Saplings	BR3	885	96	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	MH1	142	30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	MH2	440	135	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	MH3	378	45	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-
	PEF1	28	81	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	PEF2	77	123	-	-	-	-	-	-	-	-	-	-	-	A	A	A	A
	PEF3	67	36	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	SM1	543	281	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	SM2	419	217	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	SM3	172	138	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

N, number of stems; ANP, Acadia National Park; BR, Big Reed Forest Reserve; MH, Moosehorn National Wildlife Refuge; PEF, Penobscot Experimental Forest; SM, Sunkhaze Meadows National Wildlife Refuge**.**

1.4. Discussion

In this study, we combined a number of field and analytical approaches aimed at revealing the conditions under which northern white-cedar successfully regenerates and the spatial patterns created by these site conditions. Taken together, these findings shed light on general trends that influence regeneration success. Given the large number of stands exhibiting a range of regeneration conditions and a number of site-specific findings, we focus our discussion below on these general trends while acknowledging the complexity of the results. This discussion will be representative of the observed trends as they apply to most plots to varying degrees.

1.4.1. Stand Metrics

The species composition and stand structure of all our plots correspond well with the community descriptions provided by Curtis (1946) and Gawler and Cutko (2010). One exception was tamarack, which was found in the overstories of only two plots. While stand structure varied among plots, those at Big Reed exhibited basal areas, tree densities, and woody debris volumes similar to previous cedar studies at Big Reed (Fraver et al. 2020, which included one of these same plots) and regionally (Wesely et al. 2018). The remaining plots displayed similar characteristics overall; however, they generally lacked the unique combination of conditions indicative of old-growth, such as high volumes of coarse woody debris, large-diameter trees, and low tree density.

The understory species composition at our plots is also typical of this forest type (Johnston 1990, Gawler and Cutko 2010). Shrub communities commonly featured speckled alder, fly honeysuckle, sheep laurel, and winterberry holly, with the regeneration of overstory species also well-represented in this layer. Notably, cedar was the most abundant species in the

seedling layer in all plots pooled, and the same was true for 11 individual plots (the four remaining plots contained a preponderance of balsam fir and red maple). The sapling layer at all plots pooled, however, was dominated by balsam fir, with cedar being clearly dominant in only one plot and co-dominant with balsam fir, black ash, or tamarack in just three others. This shift from high abundance of cedar regeneration at smaller size classes to low abundance or low relative abundance at larger size classes is indicative of the recruitment bottleneck observed early on by many authors including Curtis (1946) and Scott and Murphy (1987) and confirmed in more recent studies (Larouche and Ruel 2015, Reuling et al. 2019).

1.4.2. Plot-level Analyses

Although our analyses focused on individual stems, we note some results at the plot level. The significant negative correlations between tree density and both seedling and sapling abundance corroborate our finding regarding canopy openness; that is, regeneration is more abundant under open canopies. The significant positive correlation between CWD volume and sapling abundance supports our findings regarding the importance of mounds (CWD formed a portion of the mounds) and/or canopy openness (CWD presence suggests past canopy-tree mortality).

1.4.3. Soil Moisture

Differences have been observed in nutrient status, species composition, and stem abundance among microtopographic features (Diamond et al. 2020), with soil moisture being a likely source of these differences (Beatty 1984, Chimner and Hart 1996). Our detailed sampling strongly supports the notion that small-scale yet meaningful differences in soil moisture exist among microtopographic positions in our study sites in summer. We can infer that, on average, plants growing in pits experience wetter conditions than those on flats, and plants on flats in turn

experience wetter conditions than those on mounds. These findings lead to conclusions regarding microsite associations of plants growing in lowland sites with highly variable microtopography and shallow depth to water table. For example, regeneration may be abundant on mounds, which allow for adequate root growth and nutrient uptake associated with unsaturated soils (Chimner and Hart 1996), or regeneration may be abundant in pits, which offer a moist refuge during droughts (Cornett et al. 1997). While our model showed microtopographic feature to be a strong predictor of soil moisture, the interactions between feature and site and between feature and plot-within-site were also significant. We attribute this to variation across plots in the size and shape of features (e.g., although not measured, pits on some plots may have been deeper than those on other plots) and differences in water table depth (also not monitored). Regardless of site-to-site and plot-to-plot variation in moisture levels among features, we conclude that at each plot the average moisture content in pits was greater than that on flats, and the average on flats was greater than that on mounds at the time measurements were taken.

1.4.4. Occurrence by Microtopographic Feature

Cedar regeneration was found more often than expected by chance on mounds, and less often on flats and pits, as demonstrated by our analysis of seedling frequency compared to the site-level proportions of the three microtopographic features. This same pattern has been noted throughout the species' range (St. Hilaire and Leopold 1995, Chimner and Hart 1996, Forester et al. 2008, Reuling et al. 2019). Mounds, which are often composed of dead wood and covered in bryophyte mats, apparently maintain moisture levels favorable to establishment and growth during most years (Curtis 1946), while offering protection from flooding common in these low-lying stands. Soil moisture on flats was more similar to that in pits than that on mounds, which could explain why seedlings were generally found less often than expected by chance on flats, as

well as in pits. The trend for regeneration to establish more often than expected on mounds was more pronounced among seedlings than saplings. Indeed, saplings at most sites were found on flats no more or less frequently than would be expected. The shift from low establishment on flats in the seedling stage to relatively greater occurrence (no more or less than expected) in the sapling stage, may indicate that the moisture conditions on flats were more favorable to success in the years between establishment and reaching the sapling stage. (We return to this topic in section 1.4.5). Sapling results at one site, SM, differ from the others, showing no deviation from expectations on any of the three features. We speculate that competition for mounds may contribute to this difference; plots at the SM site had unusually high densities of balsam fir regeneration, which has been shown to strongly favor mounds (Cornett et al. 1997). Further research is needed to determine the role of competition in cedar regeneration microsite associations.

1.4.5. Modeling Regeneration Status and Vigor

Although seedlings were found more often than expected on mounds, those seedlings established on flats seem to be at least as successful (i.e., found living) as those on mounds. This was demonstrated by our analysis of seedling status (live vs. dead), which was strongly influenced by microtopography, with live seedlings associated with flats and mounds about equally, and dead seedlings associated with pits. This finding agrees in part with previous research by Kangas et al. (2016) who found relatively high seedling survival on flats, particularly at drier sites where flats are rarely inundated. Other studies found that underlying dead wood (i.e., below the moss layer) influences seedling and sapling occurrence more strongly than does microtopographic position *per se* (Cornett et al. 1997, Rooney et al. 2002, Forester et al. 2008). Because our field protocol did not include recording dead wood underlying features, which

would have required extensive excavation, we can only speculate that similarities between seedling status on mounds and flats may have resulted in part from similar prevalence of moisture-retaining dead wood underlying these two features.

Microtopography was also related to sapling status (live vs. dead), though this variable was not as prominent in the top models of the sapling status analysis as it was in the corresponding seedling analysis. Although pits were not used in the sapling analysis due to scarcity of dead saplings in pits, results suggest that live saplings were more prevalent on flats when compared to mounds. The ability of cedar regeneration at both the seedling and sapling stages to thrive on flats suggests that, after establishment, these microsites – with soil moisture conditions intermediate between that of mounds and pits – may serve as a refuge from desiccation during drought. That is, the seasonal flooding typical in this forest type results in a shallow rooting zone near the surface (Curtis 1946, Pregitzer 1990), which is an advantage during most years. However, this shallow rooting system creates a risk of desiccation during drought periods (Curtis 1946). The importance of substrates capable of maintaining adequate moisture on the establishment and survival of seedlings has been emphasized by previous authors (Nelson 1951, Caulkins 1967). We propose that the moisture conditions of flats are particularly favorable to cedar seedlings and saplings because they protect from the inundation experienced by pits during years with typical flooding and from the desiccation experienced by mounds in drought years. Taken together, the positive association between seedling establishment and mounds but having a live status most associated with flats, coupled with greater likelihood for live saplings to be found on flats, point to possible changes in the stand conditions causing differing regeneration dynamics over time, or a common shift in microsite requirements as cedar seedlings develop into saplings.

As expected, browse was also a strong predictor of seedling status, although we were not able to include this variable in the sapling analysis. Cedar stands are important sources of shelter for white-tailed deer, particularly in winter, and cedar is reported to be highly palatable to deer (Bradshaw and Waller 2016). The capacity of deer browsing to impede or prevent cedar regeneration has been documented in controlled studies (Cornett et al. 2000; Larouche & Ruel 2015); however, attempts to link stand- and region-scale deer populations to regeneration density and survival have been inconclusive (Villemaire-Côté et al. 2017, Reuling et al. 2019). Here, we have quantified browser impact by directly linking individual plant-level browse to seedling status, demonstrating that un-browsed seedlings were more likely to be alive and browsed seedlings were more likely to be dead.

We pooled all browse identified as being caused by either ungulate or hare in these analyses due to a desire to characterize the total effect of browsing; however, we found deer or moose (*Alces alces*) (combined as ungulate browse) to be the dominant browsers overall, followed by hare (*Lepus americanus*). We note that as in previous studies of seedling browse, we were unable to tally seedlings that had been browsed to the ground, as no part of the seedling would have been visible. Although the number of such seedlings is unknown, their presence would have strengthened these results and may have revealed a more pronounced negative effect of browse on seedling success.

While microtopography and browse were the most influential predictors of seedling status, canopy openness was also a significant factor, showing a positive association in a majority of the top models. These results are similar to those of previous studies that found only slight positive associations between canopy gaps and cedar seedling densities (Rooney et al. 2002, Forester et al. 2008); however, our analysis shows a clear relationship between increased

canopy openness and the success of individual seedlings, with live seedlings tending to be more prevalent under open conditions. Sapling status was also strongly influenced by canopy openness, as a strong positive association was seen between increased canopy openness and live sapling status. The interaction between microtopography and canopy openness was present in a minority of top models in both the seedling and sapling status analyses, showing that the benefit of increased canopy openness differed among microtopographic feature, although little can be inferred from this result due to the insignificance of the interaction on its own.

Although support for crowding was not especially strong for the seedlings (crowding appeared but was not significant in half of the top models), support was stronger for the saplings (crowding was significant in the top three models). Surprisingly, crowded seedlings and saplings were more likely to be alive. This finding could be explained by the fact that seedlings and saplings were strongly clustering on favorable microsites, the benefits of which likely outweighed the negative effect of neighborhood competition. The conclusion that regeneration was clustered on favorable microsites is further supported by the clustering observed in the seedling and sapling spatial pattern analyses, and in the bivariate *L(t)* function results for saplings showing a general repulsion from trees. Another unexpected result was the overall negative association between sapling status and DBH, though this was not significant on its own. Further analyses are necessary to reveal the underlying cause of this relationship.

Results of the LCR model analysis resembled the trends seen in the sapling status models with regard to canopy openness, thus demonstrating a strong association between high sapling vigor and high canopy openness. A positive association between light levels and LCR have been observed in other forest types (Duchesneau et al. 2001). LCR also showed a negative association with crowding, at least at the crowding intensities reported here. These results support those of

previous studies (Berrill et al. 2017) and point to a decline in sapling vigor resulting from loss of lateral growing space and neighborhood competition.

1.4.6. Assessing Spatial Dependence

Cedar regeneration in both the seedling and sapling size classes was clustered spatially, as revealed by our spatial pattern analyses. While this species has a tendency to layer (Nelson 1951), which undoubtedly contributes to clustering of regeneration, this finding may also suggest a common reliance on favorable microsites. A fine-scale topographic map or digital elevation model (DEM) of each plot could be used to determine if clusters of seedlings or saplings were associated with particular microtopographic features; however, adequate DEMs were not available in the current study (a DEM exists for the PEF, but the resolution is not sufficient). Although we are unaware of other empirical studies of spatial patterning for cedar regeneration, Silla et al. (2002) reported clustering seedlings and saplings for the closely related *Fitzroya cupressoides*, also attributing this pattern to the patchiness of favorable microsites. Because most of these stands have been shaped by harvesting and thus no longer reliably reflect natural stand-development processes, we hesitate to make inferences regarding tree spatial patterning. The old-growth stands at Big Reed were the exception, showing an overall random tree arrangement. Though not affected by harvesting, the spatial patterns are influenced by patchy mortality of trees during wind storms (*personal observation*).

The increased importance of canopy openness with regard to sapling status was also born out in the bivariate *L(t)* results, where we demonstrated repulsion between cedar trees and saplings. This finding suggests that growing space away from the shade of trees is favorable to sapling establishment overall, though two of the eight plots analyze showed no repulsion for reasons that are not clear. Seedlings overall showed slight attraction to trees and saplings at a

minority of plots. This finding supports field observations of seedlings growing on the mounded bryophyte mats surrounding the bases of trees. It further emphasizes that seedlings of this shade-tolerant species are not entirely dependent on open-canopy conditions for establishment. Conversely, cedar saplings showed slight evidence of repulsion from trees, supporting our finding above that this size class benefits most significantly from greater canopy openness. These analyses also support the presumption that sapling location depends on the location of seedling establishment, due to the attraction seen between saplings and seedlings.

1.5. Management Implications

The findings presented here suggest the establishment and recruitment of cedar regeneration can be fostered using management strategies that aim to (1) allow for or create canopy conditions that promote both establishment and recruitment of cedar regeneration, (2) maintain diverse microtopography, and (3) reduce browsing impact. First, although the present study does not evaluate the role of gap size on cedar regeneration, we observed a trend showing greater canopy openness associated with both sapling vigor and increased likelihood of live seedlings and saplings. As noted in previous studies, the formation of gaps through certain silvicultural systems may effectively create high-light microsites advantageous to regeneration success (Boulfroy et al. 2012). Our results show that while both sapling and seedling live status is associated with greater canopy openness, locations of only saplings are associated with gaps or sparser canopies. Therefore, we recommend multi-aged forest structures with a light canopy thinning through single-tree selection during seedling establishment to allow for increased sunlight while mitigating the risk of increased soil desiccation or growth of competing species. After seedling cohort establishment, a gradual opening of the canopy using group selection or

irregular shelterwood may encourage growth and recruitment into larger size classes, as suggested by previous studies (Larouche et al. 2011, Ruel et al. 2014).

Our findings also support management practices that protect the natural microtopography of cedar stands, as mounds were strongly associated with occurrence of live seedlings and saplings, while flats may also contribute to sapling vigor and success. This mirrors recommendations by previous authors who noted the negative effect that harvest-related ground disturbance can have on cedar regeneration and microtopography (Chimner and Hart 1996, Cornett et al. 1997). We recommend that management activities are conducted in ways that minimize the impact of machinery on the forest floor. Minimal trails should be constructed and used, and activities should be conducted in winter when the ground is frozen and protected by snow. While our study did not address coarse woody debris as a substrate, nurse logs create mounds that are thought to provide excellent microsites for seedling establishment (Caulkins 1967). Logs and other coarse woody debris should, therefore, be retained and protected on site when possible.

Finally, because our results show that dead seedlings are associated with browsing, we recommend that managers consider excluding deer from stands managed for high production if large deer numbers are anticipated. Deer may be excluded or otherwise controlled after harvesting while new seedlings are establishing and when advance regeneration is experiencing rapid growth as it recruits to larger size classes (Verme and Johnston 1986). Leaving logging slash and other woody debris on site at time of harvest represents a simple means of partial deer exclusion, as the slash tends to limit deer access to seedlings (Verme and Johnston 1986). Protection from deer should continue until sufficient regeneration has grown beyond the reach of

deer (Hofmeyer et al. 2009). This may not be necessary in some cases, however, as deer and other browsers tend to be less abundant in recently disturbed stands and in large openings (Johnston 1977).

1.6. Suggestions for further Research

This study provides important insights into the stem-level conditions that influence cedar regeneration during both the seedling and sapling stage, including the influence of browse, canopy openness, microtopography, and neighborhood crowding, as well as the relationship between microtopography and soil moisture. Despite the detailed sampling protocol and these important insights, we recognize the limitations of the current study and provide below several suggestions for expansion of this work.

First, while the study sites spanned a large area of Maine, the addition of more sites over a broader geographic region would strengthen the analysis by providing an even wider range of stand conditions. Further, with additional sites, we could conduct more rigorous site-level analyses, which were limited by the current sample size (N=5 sites). Second, information about the growth of individuals and the events that affect stand development would be extremely valuable in interpreting regeneration use of microsites and the resulting spatial patterns. This could be accomplished through the use of dendrochronological analyses to study stand history and uncover important events that would explain the disparity between the results for the two size classes, while also providing essential information about the stand establishment and past disturbance. Alternatively, regeneration spatial patterns and the influence of microsite conditions over time could be analyzed through repeat surveys, ideally following individuals through time. Third, a more complete understanding of spatial patterning could be obtained with the help of digital elevation models to examine in detail the microtopography of each stand and how this

relates to locations of regeneration. The sizes and shapes of microtopographic features, as well as the locations of features relative to trees and canopy gaps, are needed to fully explain the clustering of regeneration.

Finally, distinguishing between stems of seed and vegetative origin is necessary to understand the degree to which layering of stems contributes to clustering and to investigate the particular effects of various microsite conditions on regeneration of seed and vegetative origin. Previous studies have documented high rates of vegetative reproduction in cedar (Curtis 1946, Nelson 1951, Caulkins 1967), primarily through layering, and this is undoubtedly an important factor. Clear instances of layering were observed during the seedling surveys at most of our plots, but the vegetative component of cedar regeneration was not addressed in this study due to the difficulty in determining the origins of seedlings without destructive sampling. Thus, regeneration of seed, layering, and indeterminate origin were treated equally, as in studies by Rooney et al. (2002) and Saucier et al. (2018). This knowledge gap could be filled in future research through examination of excavated seedlings, or the development of a method for reliably determining seedling origin in the field without the need for excavation.

CHAPTER 2

BROWSE SELECTION OF WOODY SPECIES IN UNDERSTORIES OF LOWLAND *Thuja occidentalis* L. FORESTS

2.1. Introduction

Thuja occidentalis L. (known as northern white-cedar) is a key component in many mixed forest types in northeastern North America, where it has adapted to a wide range of sites including cliffs and dune communities (Gawler and Cutko 2010). This slow-growing species, however, is notable for forming pure or nearly pure stands in lowland swamps and seeps. *T. occidentalis* is essential to a specialty timber market in which the wood is prized for its rot-resistance, durability, and ease-of-use in crafting shingles and other outdoor items (Boulfroy et al. 2012), and has long been significant to indigenous peoples in this region for practical and ceremonial purposes (Geniusz 2015). *T. occidentalis* stands also serve as habitat to several rare plants and lichens, and they provide a vital food sources to white-tailed deer (*Odocoileus virginianus* Zimmermann, hereafter deer), particularly in winter when deer gather and shelter in *T. occidentalis* stands with dense understories (Johnston 1990, Gawler and Cutko 2010).

Like many forest types in eastern North America, *T. occidentalis* stands are facing a regeneration barrier (Dey et al. 2019, Miller and McGill 2019). Declines in extent and density of *T. occidentalis* overstories have been observed over many decades and throughout the species' range (Curtis 1946, Scott and Murphy 1987, Saucier et al. 2018). *T. occidentalis* stands often contain abundant *T. occidentalis* seedlings, but saplings may be sparse (Scott and Murphy 1987, Reuling et al. 2019). This suggests a regeneration bottleneck wherein *T. occidentalis* reproduces plentifully through seed germination and layering, but these seedlings fail to recruit to larger size classes. Recruitment failures can eventually lead to shifts in overstory species composition.

Several potential factors contributing to this regeneration barrier have been proposed, including competition and unfavorable harvesting practices (Heitzman et al. 1997, Larouche et al. 2010).

Another possible cause for the *T. occidentalis* regeneration bottleneck is browsing pressure by deer. Deer populations grew sporadically throughout eastern North America during the 20th century due to shifting land use and the eradication of key predators (Cornett et al. 2000, Larouche and Ruel 2015), and this is hypothesized to have caused greater browse pressure and hence reductions in abundance of palatable species like *T. occidentalis*. Large deer populations have been associated with decreased likelihood of *T. occidentalis* recruitment (Rooney et al. 2002), and heavy browsing has been shown to reduce abundance of *T. occidentalis* seedlings (Cornett et al. 2000). The complexity of temporally variable habitat use (e.g. deer may spend much of the winter in *T. occidentalis* stands and then occupy other areas the rest of the year) and uncertain local deer population densities (available county- or region-scale densities may not reflect use of individual *T. occidentalis* stands), make it difficult to link deer population size to browsing pressure on individual stands (Villemaire-Côté et al. 2017, Reuling et al. 2019). Because of these limitations, the relationship between stand-level deer use intensity and the establishment and recruitment of *T. occidentalis* in naturally regenerating stands remains unclear.

In addition to deer, which are presumed to exert the prevailing browsing pressure in *T. occidentalis* stands, snowshoe hare (*Lepus americanus* Erxleben, hereafter hare) and moose (*Alces alces* Gray) are also sources of browsing pressure (Nelson 1951, Johnston 1990). Moose typically congregate in softwood and mixed forest types (Kearney and Gilbert 1976), which provide suitable shelter and browse (Ludewig and Bowyer 1985) and are known to occasionally occupy *T. occidentalis* stands (Thompson et al. 1995) where they typically browse on the regeneration of competing tree species. Hare are known to utilize a range of habitats including

swamps and *T. occidentalis* dominated forests (Conroy et al. 1979), though *T. occidentalis* is not thought to be preferred by hare as a food source (Tefler 1972). Still, the impact of hare browse on *T. occidentalis* regeneration must be considered due to the presence of hare in *T. occidentalis* stands and their occasional consumption of this species.

Snow depth may also play a role in role in browsing pressure, as deeper and more long-lasting winter snowpack would protect shorter seedlings from browse. In fact, a common research strategy for focusing on winter browse in temperate and boreal systems is to record browse observations only on stems above a minimum height, as stems below that height would be covered in snow for much of the winter, making them inaccessible to browsers (Beals et al. 1960, Frelich and Lorimer 1985, Cornett et al. 2000). Understanding this phenomenon can help explain the variability in regeneration abundance at different height classes; however, few empirical studies have demonstrated a relationship between seedling height and likelihood of browse in regions experiencing substantial winter snowpack.

We investigated the fine-scale impacts of multi-species browsing on the understory communities of 15 lowland *T. occidentalis* stands at five diverse sites across Maine, USA. The objectives of this study were to 1) determine if browse frequency differs by height among *T. occidentalis* seedlings, and 2) assess relative browse frequencies on common woody species in these stands due to deer, moose, and hare. Data for this study were collected as part of a study of site factors influencing *T. occidentalis* regeneration. Results from this work will fill an ongoing knowledge gap regarding woody species selection among browsers in *T. occidentalis* stands and the effect of selective browsing on the understory woody communities, helping land managers to maintain *T. occidentalis* forest regeneration and recruitment processes.

2.2. Methods

2.2.1. Study Sites

This work was conducted at five forested sites located in north, central, and eastern Maine, USA, that were known to include substantial *T. occidentalis* populations and are currently set aside from harvesting (Figure 7). Sites include Acadia National Park (ANP), Big Reed Forest Reserve (BR), Moosehorn National Wildlife Refuge (MH), the Penobscot Experimental Forest (PEF), and Sunkhaze Meadows National Wildlife Refuge (SM) (Table 12, Appendix). The Big Reed Forest Reserve represents old-growth (never harvested) conditions (Fraver et al. 2009); the remaining sites have been previously harvested. At each site we selected three suitable stands that met the following criteria: 1) relative *T. occidentalis* basal area > 65%, 2) area large enough to accommodate a 35 × 35 m research plot, given that *T. occidentalis* stands in this region often occur as 'micro-stands' (*sensu* Boulfroy et al. 2012), and 3) no recent history of harvest (cut stumps, if present, were in advanced stages of decay). These criteria ensure sites used in the study demonstrated examples of natural *T. occidentalis* regeneration dynamics. The resulting stands represent a range of forest structures and regeneration conditions, though this was not specified in our selection criteria.

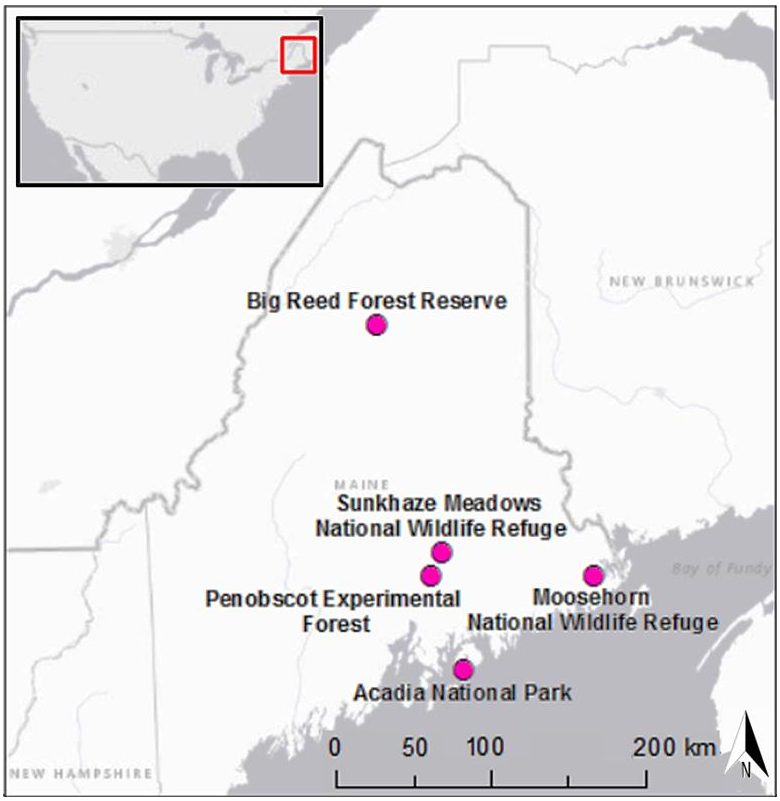

Figure 7. Site locations. Five study sites in Maine, USA

T. occidentalis dominates the canopy layer of all stands, with *Picea rubens* Sarg. (red spruce) and *Abies balsamea* (L.) Mill (balsam fir) also common in the canopies. Shrub communities consist of patchy populations of several deciduous, mostly short shrubs, with *Kalmia angustifolia* L. (sheep laurel), *Alnus incana* (L.) Moench (speckled alder), and *Lonicera canadensis* W Bartram ex Marshall (fly honeysuckle), being the most common species. The herbaceous understories of these stands are generally sparse and presumed largely inconsequential with regard to tree species regeneration. Nevertheless, substantial fern and graminoid communities are present at four plots. Ground cover largely consists of bryophyte mats and litter. Details regarding woody species composition at the tree, sapling, and seedling size classes can be found in Table 15, Table 16, and Table 17 in the Appendix.

The five study sites range in elevation from 36 m a.s.l. at ANP, located on Mount Desert Island, to 372 m a.s.l. at BR in the northern Maine highlands (U.S. Geological Survey, 2018) (Table 7). Annual precipitation ranges from 1073 to 1352 mm, and mean annual temperature ranges from 3.5 to 7.5°C (PRISM, 2020, 30-year normals). Snow depth is presented in Table 7 as a mean of maximum winter snow depths derived from maps of interpolated data from snow measurement sites located throughout Maine during the three winters prior to our field sampling (Maine Geological Survey 2020). The northernmost site (BR) shows the greatest snow depths at 70-85 cm, and the site on Mount Desert Island (ANP) shows the lowest snow depths at 25-40 cm. Soils are deep, poorly-drained mucky peats or decomposed plant material with lower horizons composed of loam or muck (Web Soil Survey, 2020). As is typical of this forest type, these sites have well-developed pit-and-mound (or hummock-and-hollow) microtopography (Gawler and Cutko 2010). Seasonal flooding in this forest type is not uncommon (Thompson and Sorenson 2005).

Table 7. Site locations and characteristics. Elevation data from U.S. Geologic Survey digital elevation model. Climate data based on 30-year normals from 1981 to 2010, sourced from PRISM Climate Group, Oregon State University. Snow depth expressed as a mean of the maximum winter snow depths over three years (2017-2019), sourced from the Maine Geological Survey. NWR, National Wildlife Refuge; EF, Experimental Forest.

Site	Site Abbrev.	Lat., Long.	Elevation (m)	Annual Precip. (mm)	Mean Annual Temp. (°C)	Max. Snow Depth (cm)
Acadia National Park	ANP	44°17' N, 68°22' W	36	1352	7.5	25-40
Big Reed Forest Reserve	BR	46°21' N, 69°03' W	372	1082	3.5	70-85
Moosehorn NWR	MH	44°51' N, 67°14' W	37	1267	6.2	45-60
Penobscot EF	PEF	44°50' N, 68°37' W	41	1073	6.4	40-55
Sunkhaze Meadows NWR	SM	44°59' N, 68°31' W	40	1098	6.4	40-55

Deer and moose are found throughout the state of Maine, but population densities vary spatially. Deer are much more abundant in the central and southern portions of the state where the ANP, MH, PEF, and SM sites are located, whereas moose are more abundant in the northern and eastern portions where the BR site is located (Maine Department of Inland Fisheries and

Wildlife 2019 b). Numbers of moose and deer harvested from the towns in which each site is located during the year of field sampling and the previous 4 years are listed in Table 8. Towns range in size from 3.5 km^2 (Southwest Harbor) to 131.1 km^2 (Bradley) (U.S. Census Bureau 2010). These data are intended to provide a rough estimate of the relative population densities of the two species and to demonstrate browser population differences across the study area. Although harvest data do not provide definitive, site-specific ungulate population density estimates, they do provide some predictive ability, particularly for small geographic areas like the towns in which our sites are located, and for larger ungulate populations like Maine's deer herds (Pettorelli et al. 2007, Imperio et al. 2010).

Table 8. Harvest records. Deer and moose harvested in the towns in which each site is located during the year of our field surveys and the four previous years. More deer than moose were harvested from the four southern sites, while the opposite is true of the northernmost site at Big Reed. Data from the Maine Department of Inland Fisheries and Wildlife. ANP, Acadia National Park; BR, Big Reed Forest Reserve; MH, Moosehorn National Wildlife Refuge; PEF, Penobscot Experimental Forest; SM, Sunkhaze Meadows National Wildlife Refuge.

Site	Town or	2015		2016		2017		2018		2019		Average	
	Township	Deer	Moose	Deer	Moose	Deer	Moose	Deer	Moose	Deer	Moose	Deer	Moose
ANP	Southwest Harbor	4	0	5	0	1	0	2	0	1	0	2.6	0.0
BR	T8 R10 WELS	2	4	2	2	1	5	0	3	1	8	1.2	4.4
MH	Edmunds	2	1	5	0	9	0	12	0	7	1	7.0	0.4
PEF	Bradley	25	1	33	1	31	0	26	3	26	2	28.2	1.4
SM	Milford	10	1	51	0	21	0	32	0	40	0	30.8	0.2

To incorporate a finer-scale potential predictor of deer use intensity, we note that all stands at two of our sites (ANP and SM) are in areas designated by the Maine Department of Inland Fisheries and Wildlife (MDIFW) as deer wintering areas (MDIFW 2019 a). Deer wintering areas (DWA) are identified by the MDIFW as areas with softwood shelter of the types known to be favored by deer in winter. Despite these designations, we cannot confirm these areas are, in fact, used as wintering areas by deer. For example, the DWAs at ANP are not likely to be used as such due to the low snow depths documented on Mount Desert Island, as well as observations of low seasonally specific habitat use by deer in ANP (Fuller and Harrison 2009),

though deer have historically been known to gather in wintering areas in this region (Allen 1970). A management plan is established at SM for the protection of the DWA delineated by the MDIFW for winter use by deer (U.S. Fish and Wildlife 2013), though it is not confirmed that deer overwinter in these areas. Despite the uncertainties inherent in DWA designations, and the known spatial and temporal variation in deer herd densities (Villemaire-Côté et al. 2017), we regard these habitat designations as potentially useful in explaining browser impacts.

Finally, hare are common throughout Maine's forests wherever there are dense understories providing adequate cover, though their populations fluctuate over the course of several years (Jakubas and Cross 2002). We are not aware of any predicable geographic pattern in hare population densities.

2.2.2. Data Collection

All plot sampling was completed between May and August of 2019. At each of the five sites, we inventoried three stands, and within each stand we established one 35 × 35 m plot. Attempts were made to place plots in the geographic center of the stands oriented such that plot borders followed cardinal directions. However, when stand size, stand shape, property boundary, or other constraints precluded such placement, plots were shifted or oriented differently to avoid these obstacles. Plot borders were demarcated with tape measures. In the center of each of these full plots, we established a 15 × 15 m interior plot for more detailed inventory of seedlings and saplings.

All trees with a diameter at breast height (DBH, 1.4 m) ≥ 10 cm in the full plot were inventoried, recording DBH, species, and status (live or dead). Diameters of saplings (individual live stems of tree and shrub species taller than 1.4 m and DBH < 10 cm) in the interior plot were measured in the same manner as trees and presence of browse was recorded. Browse presence or

absence was recorded as well as apparent browser (ungulate or hare). Hare browse was identified as clean, 45° shears, and ungulate browse was identified as jagged tears, as described by Pierson and DeCalesta (2015). Examples of ungulate and hare browse are shown in Figure 12 (Appendix), illustrating distinct differences in appearance that allowed us to confidently identify browser in most cases. Only live branches were examined to focus on browse of the current year's stems and foliage, and only those branches with any part below 2 m were examined as anything above that height is considered out of reach of deer (Beals et al. 1960). Recognizing that moose may reach branches greater than 2 m in height, we note anecdotally that no browse was observed on any branches above that cut-off. Saplings with no live branches within reach were not included.

Seedlings of tree and shrub species were measured (height, nearest cm) in the interior plot. Seedlings were defined as individual live stems of tree and shrub species (excluding subshrubs) between 15 and 140 cm in height. The lower limit was intended to exclude the ephemeral seedling bank, allowing us to evaluate only established seedlings. However, due to the tendency for small *T. occidentalis* seedlings to become prostrate and root along the stem, *T. occidentalis* seedlings shorter than 15 cm were considered established and were included in the survey if they produced at least three branches with scale-like (mature) foliage (adapted from Curtis 1946). Browse class and browse type were recorded as for saplings.

2.2.3. Analysis

2.2.3.1. Browse by Height Class

We sought to evaluate the assumption that short seedlings experience lower rates of browsing in areas with persistent and deep snow. We thus categorized *T. occidentalis* seedlings (ranging in height from 2 to 139 cm) into 10 cm height classes, and then calculated and graphed

the percent browse by height class. Other species were not used in this analysis because they comprise a narrower range of heights due to the different sampling protocol. Seedlings from all sites were pooled due to low numbers of seedlings in some height classes at individual sites. We tested if the observed distribution of browse by height class differed from that of a uniform distribution (equal browse at all height classes) using the Kolmogorov-Smirnov two-sample test.

2.2.3.2. Species Selection

We use chi-squared goodness-of-fit tests to determine frequency of browse in both the seedling and sapling size classes. To evaluate the relative browse impact on *T. occidentalis* and its competitors, we limited these analyses to the species presumed to exert the greatest influence on *T. occidentalis* regeneration on the basis of abundance (>50 seedlings per species in the site-pooled dataset, and >20 seedlings per species in at least one plot). We included only tree species plus one shrub species that was especially abundant and is known to reach tree-height in other parts of its range. These tree species, in addition to *T. occidentalis*, were the softwoods *A. balsamea*, *Larix laricina* (Du Roi) Koch (tamarack), *P. rubens*, and *Tsuga canadensis* (L.) Carrière (eastern hemlock), the hardwoods *Acer rubrum* L. (red maple), *Betula alleghaniensis* Britton (yellow birch), and *Fraxinus nigra* Marshall (black ash), and the shrub species *A. incana*. To ensure that the lower height limit of *T. occidentalis* seedlings did not confound the analyses, *T. occidentalis* seedlings shorter than 15 cm were excluded so that the datasets for each species comprised the same potential height range.

We performed chi-squared tests to compare the number of individuals browsed of each species to the species' total abundance, where the null hypothesis expects that species are browsed in frequencies equal to their relative abundance. For the seedling and sapling overall analyses, both browse types (hare and ungulate) were included, and species abundance and

browse frequencies were pooled across all plots to capture the general trend of browse selection throughout the study area. Sub-analyses were performed to characterize various aspects of browse selection, and each analysis was applied to seedlings and saplings separately.

Hare browse selection was calculated using frequencies of stems recorded as having been browsed by hares from all plots pooled, as we expected hare to be present throughout the study area without following predictable geographic patterns. Ungulate browse at only the BR site (higher moose harvest plots) was analyzed to characterize browse selection assumed to be attributable primarily to moose. This assumption was based on harvest records that suggest moose are more abundant than deer at this site (MDIFW 2019 b), as well as anecdotal observations of moose (but not deer) scat in the three stands during sampling. Deer browse selection was calculated two ways. First, we calculated browse selection using only stems browsed by ungulates at the two sites classified as containing habitat favorable for deer wintering areas (ANP and SM, designated cover plots) (MDIFW 2019 a). Consistent with harvest data, we assumed the ungulate browse at these plots was predominantly deer, and we also consider the possibility that these sites are more likely to experience heavy use in winter than sites not designated as deer wintering areas. Second, we analyzed ungulate browse at the two sites having a majority of deer harvests but not classified as deer wintering areas (MH and PEF, higher deer harvest plots). Again, we assumed that ungulate browse at these plots was predominantly deer; however, they may demonstrate browse characteristics unlike that of the plots known to contain cover suitable for deer-yards. For each of the above analyses, we plotted the chi-squared test residuals against the overall abundance of the species to visualize the deviation of the observed from the expected browse frequencies.

2.3. Results

2.3.1. Site Descriptions

T. occidentalis clearly dominated all sampled stands, its relative basal area ranging from 67% at plot PEF3 to 94% at plot BR2. Table 9 provides structural details for all plots, and Table 15 (Appendix) presents relative basal areas of all tree species, all plots. Common tree and shrub species accompanying *T. occidentalis* in the understory (sapling and seedling layers) included *A. balsamea, A. rubrum, P. rubens, A. incana, L. laricina, F. nigra, B. alleghaniensis, K. angustifolia, L. canadensis, T. canadensis, Gaylussacia baccata* (Wangenh.) K. Koch, *Ilex mucronata* (L.) Powell, Savolainen & Andrews, and *I. verticillata* (L.) A. Gray, listed in decreasing abundance, stands pooled (Table 16 and Table 17, Appendix).

Table 9. Stand summary metrics. Organized alphabetically by site. BA, basal area; NWR, National Wildlife Refuge.

Site Plot	**BA** (m^2 ha^{-1})	**Stems** (trees ha^{-1})	**DBH (cm)** mean (SD)	***T. occidentalis*** **rel. BA (%)**
Acadia National Park				
ANP1	41.5	1282	19.6 (5.2)	85.9
ANP2	50.0	1486	19.5 (6.9)	88.7
ANP3	30.8	727	21.9 (7.8)	78.9
Big Reed Forest Reserve				
BR1	58.6	686	28.3 (17.0)	91.8
BR2	62.8	857	26.7 (14.9)	93.9
BR3	48.8	751	25.6 (13.1)	81.1
Moosehorn NWR				
MH1	61.3	971	26.9 (9.0)	86.8
MH2	42.4	1078	21.2 (7.4)	92.3
MH3	47.2	1004	22.7 (9.2)	68.9
Penobscot Experimental Forest				
PEF1	62.8	1951	19.5 (5.5)	93.4
PEF2	52.5	1641	19.0 (6.7)	68.1
PEF3	38.4	1404	17.8 (5.5)	67.0
Sunkhaze Meadows NWR				
SM1	39.6	873	22.3 (9.0)	82.1
SM2	44.6	1176	20.7 (7.2)	85.3
SM3	62.8	1306	23.3 (8.3)	78.0

2.3.2. Browse by Height Class

We found a positive relationship between height and percent of browsed seedlings (Figure 8). The distribution of browse by height class differed from a uniform distribution (Kolmogorov-Smirnov D=0.132, P< 0.01). Browse frequency ranged from 3% to 14%, with seedlings in the shortest height class (0-9 cm) being the least likely to be browsed and seedlings in the 110-119 cm height class the most likely to be browsed. Browse frequency increased steadily among seedlings from 0 up to 50 cm in height, with each successive height class being browsed more than the previous. Browse continued to increase above 50 cm, but the trend was more erratic.

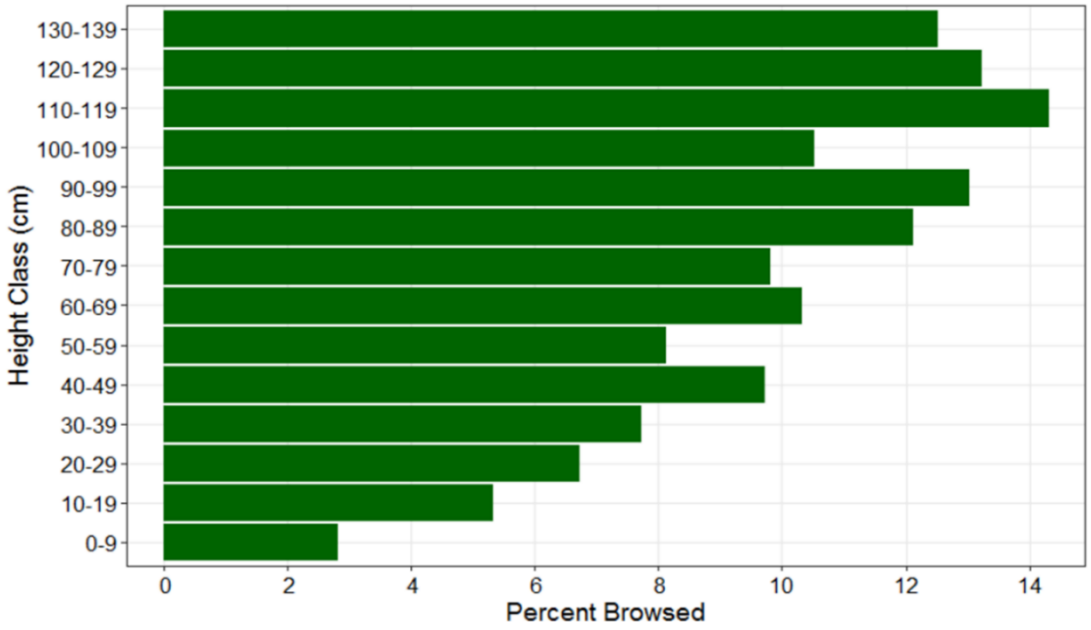

Figure 8. Browse frequency by height class. Percent of live *T. occidentalis* seedlings browsed by 10-cm height classes. Taller seedlings are more likely to be browsed than shorter seedlings. This distribution differed from a uniform distribution (Kolmogorov-Smirnov D=0.132, P< 0.01).

3.3.3. Species Selection

Results of the chi-squared goodness-of-fit tests examining browse selection of tree and shrub species in the seedling and sapling size classes are presented in Table 10 and Table 11, respectively. Species within each analysis are ordered from greatest to least percent of

individuals browsed. Positive residuals represent browse frequencies that are greater than expected given the abundance of that species, and negative residuals represent browse frequencies that are less than expected. A species with a residual of 0 is browsed at a rate equal to that species' abundance. The majority of individual species within each sub-analysis resulted in significant *P*-values (alpha ≤ 0.05). Exceptions include seedling hare browse which showed significant browse frequencies for only four of nine species, as well as sapling hare browse and sapling ungulate browse at the higher moose harvest and higher deer harvest plots (BR, MH and PEF respectively) in which browse frequencies were not significant for any species.

Table 10. Seedling browse frequency by species. Species abundance and frequency of browsed stems in the seedling size class, and results of chi-squared goodness-of-fit tests analyzing the frequency of browsed stems. Species are ordered from greatest to least percent of stems browsed. Positive and negative chi-squared residuals indicate browse frequencies greater or less than expected given relative abundance, respectively. Sub-analyses aim to characterize total browse pressure across the study area (all browse, all plots) and the impact of individual species (hare or ungulate browse at appropriate plots).

Species	Total Seedlings	Browsed Seedlings	Percent Browsed	Residual	*P*-value
all browse, all plots					
Acer rubrum	751	278	37.0	19.3	<0.01
Alnus incana	209	67	32.1	8.1	<0.01
Fraxinus nigra	103	30	29.1	4.9	<0.01
Betula alleghaniensis	58	16	27.6	3.4	<0.01
Tsuga canadensis	148	14	9.5	-0.6	0.57
Larix laricina	251	22	8.8	-1.1	0.29
Thuja occidentalis	4743	384	8.1	-8.7	<0.01
Abies balsamea	1737	112	6.4	-6.2	<0.01
Picea rubens	562	24	4.3	-4.9	<0.01
hare browse, all plots					
Acer rubrum	751	126	16.8	16.5	<0.01
Betula alleghaniensis	58	7	12.1	2.8	<0.01
Fraxinus nigra	103	12	11.7	3.5	<0.01
Tsuga canadensis	148	10	6.8	1.5	0.13
Larix laricina	251	16	6.4	1.7	0.09
Abies balsamea	1737	59	3.4	-1.7	0.08
Picea rubens	562	18	3.2	-1.1	0.25
Alnus incana	209	5	2.4	-1.3	0.21
Thuja occidentalis	4743	104	2.2	-9.8	<0.01
ungulate browse, higher moose harvest plots (BR)					
Alnus incana	150	28	18.7	7.3	<0.01
Acer rubrum	89	15	16.9	4.8	<0.01
Betula alleghaniensis	52	8	15.4	3.2	<0.01
Abies balsamea	210	16	7.6	1.8	0.07
Fraxinus nigra	23	1	4.3	-0.1	0.91
Thuja occidentalis	1669	44	2.6	-7.7	<0.01
Picea rubens	95	0	0.0	-2.0	0.03
ungulate browse, designated cover plots (ANP & SM)					
Alnus incana	56	33	58.9	11.3	<0.01
Acer rubrum	197	37	18.8	5.5	<0.01
Thuja occidentalis	2204	190	8.6	2.9	<0.01
Abies balsamea	763	23	3.0	-4.9	<0.01
Tsuga canadensis	122	3	2.5	-2.0	0.04
Larix laricina	245	6	2.4	-2.9	<0.01
Picea rubens	424	6	1.4	-4.8	<0.01
ungulate browse, higher deer harvest plots (MH & PEF)					
Acer rubrum	465	100	21.5	10.9	<0.01
Fraxinus nigra	76	16	21.1	3.8	<0.01
Thuja occidentalis	870	46	5.3	-3.3	<0.01
Tsuga canadensis	26	1	3.8	-0.7	0.47
Abies balsamea	764	13	1.7	-7.3	<0.01

Table 11. Sapling browse frequency by species. Species abundance and frequency of browsed stems in the sapling size class, and results of chi-squared goodness-of-fit tests analyzing the frequency of browsed stems. Species are ordered from greatest to least percent browsed. Positive and negative chi-squared residuals indicate browse frequencies greater or less than expected given relative abundance, respectively. Sub-analyses aim to characterize total browse pressure across the study area (all browse, all plots) and the impact of individual species (hare or ungulate browse at appropriate plots).

Species	Total Saplings	Browsed Saplings	Percent Browsed	Residual	*P*-value
all browse, all plots					
Fraxinus nigra	34	11	32.4	2.6	0.01
Alnus incana	75	17	22.7	2.0	0.05
Thuja occidentalis	174	33	19.0	1.9	0.06
Abies balsamea	627	69	11.0	-3.0	0.00
Picea rubens	33	0	0.0	-2.2	0.03
hare browse, all plots					
Abies balsamea	627	11	1.8	1.0	0.34
Thuja occidentalis	174	3	1.7	0.3	0.78
Alnus incana	75	0	0.0	-1.1	0.27
Fraxinus nigra	34	0	0.0	-0.7	0.47
Picea rubens	33	0	0.0	-0.7	0.48
ungulate browse, higher moose harvest plots (BR)					
Abies balsamea	26	11	42.3	1.7	0.09
Alnus incana	56	14	25.0	0.1	0.91
Thuja occidentalis	81	16	19.8	-1.0	0.32
Fraxinus nigra	22	4	18.2	-0.6	0.57
ungulate browse, designated cover plots (ANP & SM)					
Thuja occidentalis	41	8	19.5	2.1	0.04
Abies balsamea	475	40	8.4	-2.1	0.04
ungulate browse, higher deer harvest plots (MH & PEF)					
Thuja occidentalis	52	6	11.5	1.3	0.20
Abies balsamea	126	7	5.6	-1.3	0.20

Among the seedling browse selection analyses, hardwoods (*A. rubrum, F. nigra,* and *B. alleghaniensis*) and the shrub species (*A. incana*) were consistently selected at greater frequencies than softwood species (*T. occidentalis, A. balsamea, T. canadensis, L. laricina,* and *P. rubens*). Exceptions appear in the analysis of ungulate browse in higher moose harvest plots where *A. balsamea* was selected at higher frequencies than *F. nigra,* though the results for neither species differed significantly from expectations. Browse on *A. balsamea* seedlings was low overall, but peaked at 6.4% browsed by ungulates in the higher moose harvest plots. *T.*

occidentalis was a lesser selected species across most analyses, with only *A. balsamea* and *P. rubens* being selected at lower frequencies in the analysis of all browse at all plots (Table 10). *T. occidentalis* showed the lowest and second lowest frequency of browse in the seedling hare and moose analyses, respectively. The two seedling analyses of ungulate browse in the higher deer harvest and designated cover plots (MH and PEF, ANP and SM, respectively) showed greater percent browse of *T. occidentalis* than did the hare and moose analyses. The analysis of designated cover plots demonstrated the greatest browse frequency of *T. occidentalis* compared to all other seedling analyses.

The two sapling browse analyses with significant results (all browse at all plots and ungulate browse at designated cover plots) showed trends similar to those seen in the seedling analyses (Table 11). The frequency of browse on saplings was typically much greater than that of seedlings, but the chi-squared residuals were generally less significant due, at least in part, to the relatively low abundance of saplings. All sapling browse at all plots showed higher selection of *F. nigra* and *A. incana*, while *P. rubens* was not browsed at all. Both analyses also showed *T. occidentalis* browsed more often than *A. balsamea*.

In order to graphically represent and summarize the findings above, the natural-log-transformed abundances of each species were plotted against the residuals of the chi-squared tests (Figure 9). In these plots, a residual of 0 indicates that the frequency of browsed individuals of a species is equal to that species' relative abundance. Positive or negative residuals indicate more or less browse than expected, respectively. Analyses of species with no significant results are not shown.

Seedlings of hardwood and shrub species were always browsed more than expected, with the exception of *F. nigra*, which was just below the residual = 0 line in the higher moose harvest

plot analysis. *P. rubens* was always browsed less than expected, while the other softwood species varied in selection. The hare browse analysis showed high selection of *A. rubrum* and low selection of *T. occidentalis*, while the remaining species showed only weak deviations from expected browse rates. The moose browse analysis showed the only instance of *A. balsamea* being browsed more than expected, with this species being browsed more than other softwood species and one hardwood species. Ungulate browse at the higher deer harvest and designated cover plots showed a strong selection of hardwoods and shrubs, while softwoods were always browsed less than expected, with the exception of *T. occidentalis* in designated cover plots. *T. occidentalis* was the least selected seedling species in the overall, hare, and moose analyses, but it was selected over *A. balsamea* at the higher deer harvest plots. *T. occidentalis* was also selected over all other softwoods in the designated cover plots.

The one hardwood and one shrub species were selected over the softwood species in the overall sapling analysis. This finding is similar to the corresponding seedling analysis, with the exception of *T. occidentalis* which was selected at rates comparable to that of the hardwoods and shrubs. Ungulate browse in the designated cover plots also showed a pattern similar to that of saplings overall, with *T. occidentalis* being selected over *A. balsamea*.

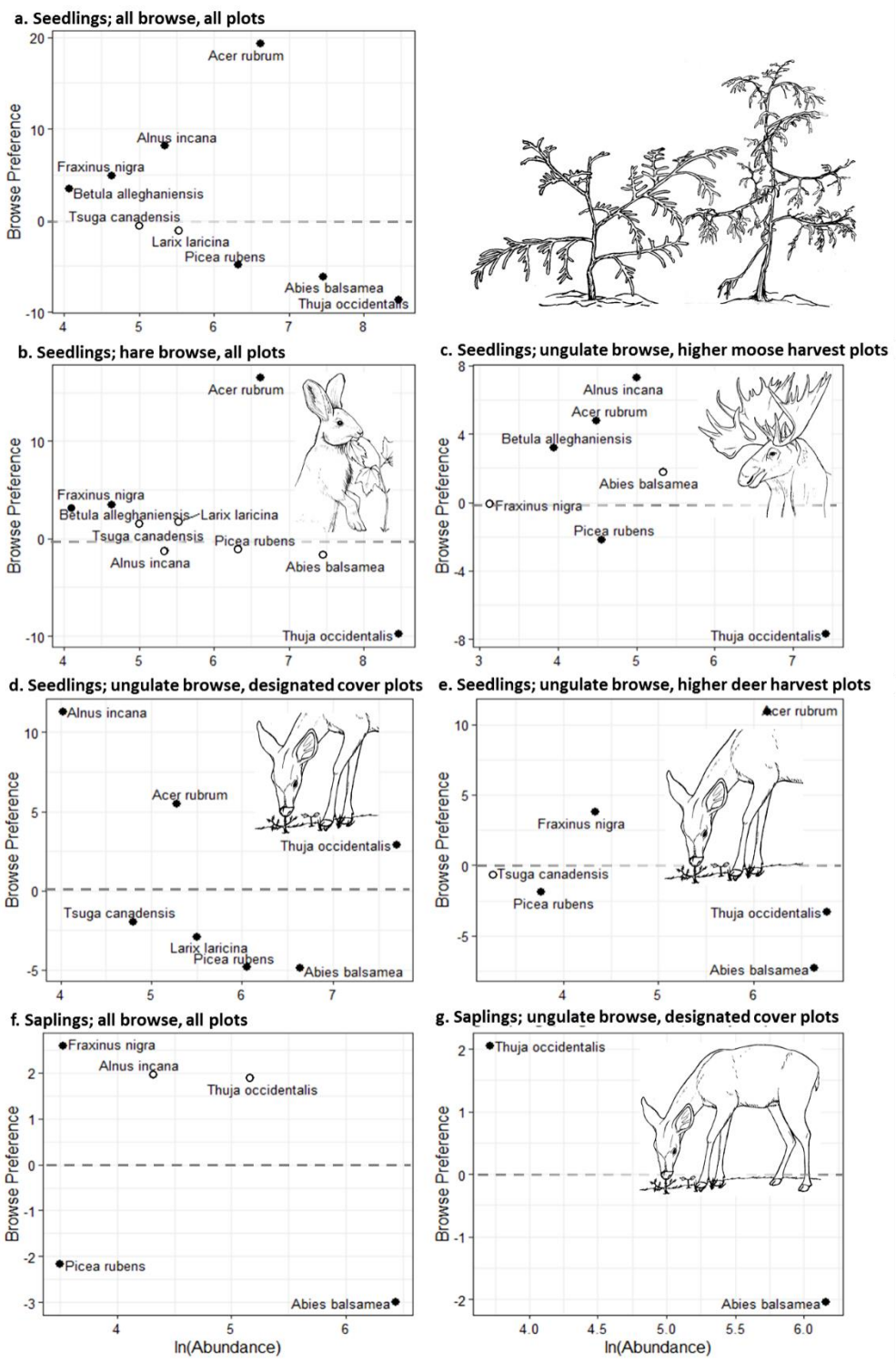

Figure 9. Browse selection. Chi-squared residuals analyzing species abundance vs. frequency of browsed stems, plotted against species abundance in seedling and sapling size classes. Dashed lines indicate frequencies of browse proportional to species abundance. Values above or below the dashed line indicate browse greater or less than expected, respectively. Closed circles indicate significant results; open circles indicate non-significance. Note: scale of vertical axis differs among panels. Illustration credit: J. Allogio.

2.4. Discussion

We found that browse increases steeply across the shortest height classes (0-49 cm), as is expected if these shortest seedlings are protected by snow cover during winter. We have no direct snow depth measurements at the stands used in this study, so we consider several indirect data sources to estimate depth. First, the Maine Geological Survey (2020) provides snow depth estimates periodically throughout winter displayed as interpolated maps based on measurements from snow measurement sites located across the state. This source shows maximum winter snow depths ranging from 25-40 cm at Acadia National Park to 70-85 cm at Big Reed Forest Reserve. These data, however, are based on weather stations located in open areas, and as a result they likely overestimate the snow depths found under the dense vegetation of our study sites. Snow depths were measured in the stand that contained plot PEF1 during mid- to late-February of 2019 (the winter prior to our field season), and the greatest depth measured in that period was 21 cm (USFS Northern Research Station, unpublished data). The Maine Geological Survey, however, reports snow depths of 30-45 cm during the nearest available time frame (March 1-6, 2019) Second, as a general guideline we refer to the work of Hodgkins and Dudley (2006) who observed typical maximum winter snow depths in Maine ranging from 50 to 80 cm in open sites, with the lowest depth being found along the coast and the greatest depth in the western mountains. Finally, direct measurements of snow depth in areas similar to our study sites can be found in the literature. The central Maine spruce-fir and *T. occidentalis* stands used by Crawford (1982) were very near our PEF and SM sites, where snow depths were described as ‘moderate’ at 30-50 cm. Ditchkoff and Servello (1998) also recorded snow depths in central Maine, where they report 61 cm of snow under softwood canopies. Taken together, these three sources of maximum

snow depth estimates from across the study area range from 25 cm to 85 cm, with an average estimate of about 50 cm, though these are likely over-estimates.

Our finding of low browse frequency on shorter cedar seedlings suggests that snow may protect short seedlings from browse, and the trend in browse percent roughly aligns with snow depth estimates. The shortest height class (0-9 cm) experienced the least browse, and the four shortest height classes (0-39 cm) experienced less browse than all taller height classes. At heights greater than 39 cm, percent browse generally increases, being relatively stable from 40-79 cm, and then continuing to increase erratically This distribution suggests that seedlings below 79 cm tall are somewhat protected from browsing, with the greatest protection offered to those below 40 cm. This depth is roughly consistent with the estimated maximum winter snow depths of about 50 cm across the study area, recognizing that some sites may experience maximum snow depths as low as 25 cm or as high as 85 cm. Similar results were found in a previous study at the PEF site, where the likelihood of browse on *T. occidentalis* seedlings increased with height class from 0-61 cm in height (Berven 2009). These results also support the assumption made by many researchers that winter browse can be assessed by excluding observations of browse on seedlings shorter than the estimated average snow depth (Beals et al. 1960, Frelich and Lorimer 1985, Cornett et al. 2000).

Our analysis of browse selection showed an overall higher frequency of browse for hardwoods and shrubs, and lower frequency of browse for softwoods. The most abundant seedling species, *T. occidentalis*, appeared as the least selected species of all browse at all plots, though the frequency of browse on *T. occidentalis* was greater than the conifers *A. balsamea* and *P. rubens*. Regarding saplings, *T. occidentalis* was selected over other softwoods by all browsers at all plots in terms of both the chi-squared test and percent browsed. The source of this shift – *T.*

occidentalis seedlings were selected less than *T. occidentalis* saplings – is not clear, but we propose that snow cover may contribute to this apparent discrepancy. As demonstrated above, seedlings as tall as 80 cm may be protected by snow during winter when deer are known to browse heavily in some *T. occidentalis* stands (Crawford 1982).

Across all plots, hare browsed *A. rubrum* at a frequency higher than expected based on stem density, and *T. occidentalis* at a frequency lower than expected, while all other species were browsed at rates roughly equal to their abundance. Disproportionate browsing of *A. rubrum*, a moderately abundant species at our study sites, is within the range of results seen in previous studies that demonstrate modest (Conroy et al. 1979) and high (Jakubus and Cross 2002) hare consumption of this species. The low browse frequency observed for *T. occidentalis* in the current study is not consistent with literature compiled by the MDIFW (Jakubus and Cross 2002), which reports a high preference for *T. occidentalis* by hare, nor with a previous study conducted at the PEF site, which reports moderate hare browse on *T. occidentalis* (Berven 2009). This apparent discrepancy may be due to a difference in browse community: the studies cited above were not limited to *T. occidentalis* forests, and they included understory species composition and abundances unlike those of our study sites. Given different plant species composition and abundance, browsers are likely to exhibit different browse selection (Cornett et al. 2000).

Ungulate browse of seedlings at the higher moose harvest plots (plots at BR) showed that frequency of browsing was greater than expected based on seedling density for the one shrub species analyzed, *A. incana*. Among the less frequently browsed softwood species, *A. balsamea* was browsed more than expected based on seedling density, while *T. occidentalis* was browsed much less than expected. These were the only results showing *A. balsamea* to be browsed more

than expected based on its abundance. Selection of *A. balsamea* is consistent with the well-documented reliance of moose on this conifer (Ludewig and Bowyer 1985, Routledge and Roese 2004). Likewise, the minimal impact on *T. occidentalis* regeneration by moose is corroborated by similar findings from Ludewig and Bowyer (1985). These findings suggest that moose were the primary browsing ungulates at this site.

The plots used in both the higher deer harvest and designated cover analyses are located in towns assumed to have greater deer population densities and browsing pressure (as opposed to moose), and the designated cover plots were additionally classified as containing habitat suitable for deer wintering areas. Acknowledging the limitations of the deer wintering area designations for predicting deer population densities (see Methods), we note that seedlings at the designated cover plots showed the highest ungulate browse selection for the least abundant species, *A. incana*, followed by *A. rubrum*. Among softwoods, frequency of browse was higher than expected for *T. occidentalis* and lower than expected for *A. balsamea*. Ungulate browse in the designated cover plots was notably the only seedling analysis that showed *T. occidentalis* being browsed more than expected. The sapling analysis in the same designated cover plots showed a similar trend for these two softwood species. In contrast, seedlings in the higher deer harvest plots not designated as deer wintering areas did not experience similar ungulate browse on *T. occidentalis*, and only hardwoods were browsed more than expected.

The results of the higher deer harvest and designated cover plot analyses are generally consistent with previous studies. High deer consumption of *A. rubrum* is well-documented (Crawford 1982, Dumont et al. 2005) and was demonstrated by the disproportionately high browse of the species in all of our relevant ungulate browse analyses. Selection of *A. balsamea* at a lower rate than expected, as seen in higher deer harvest and designated cover plots, was

anticipated, as this species is generally regarded as unpalatable to deer (Ditchkoff and Servello 1998, Dumont et al. 2005). We also recognize possible seasonal trends in deer browse, as deer are known to eat a wider variety of herbaceous vegetation, hardwood leaves, and mushrooms from spring to fall while relying more on the palatable shoots of *T. occidentalis* during winter (Crawford 1982). If the designated cover plots are indeed more heavily browsed by deer in winter than the higher deer harvest plots, then the greater selection for *T. occidentalis* seen in the former would be explained by the high winter consumption of this palatable species. Similarly, the overall high selection for hardwoods and *A. incana* might be due to a year-round consumption of hardwood leaves and shoots.

The negative effects of browse on *T. occidentalis* regeneration abundance and survival have been described in past studies, citing this as a possible or likely source of the regeneration failure seen in some *T. occidentalis* stands (Curtis 1946, Verme and Johnston 1986, Heitzman et al. 1999). Our own work in Thesis Chapter 1 revealed that browse was one of the strongest predictors of seedling status (live or dead), with non-browsed seedlings more likely to be alive. Selective browsing of palatable species can alter forest species composition (White 2012), and controlling populations of deer, in particular, is often recommended as a strategy to encourage more vigorous *T. occidentalis* regeneration (Verme and Johnston 1986, Boulfroy et al. 2012).

Despite the known detrimental effects of browsing and the preference for *T. occidentalis* by deer (Crawford 1982, Ditchkoff and Servello 1998), the results of this study only partially support the notion that browse in general, or deer browse specifically, are major determining factors in limiting *T. occidentalis* regeneration success. *T. occidentalis* was the most abundant species in the seedling size class overall and in each of the individual browser analyses, yet it was browsed less than expected in all sub-analyses except in the case of ungulate browse in plots

classified as having cover suitable for deer wintering. Additionally, in none of the analyses was *T. occidentalis* selected at a higher rate than any hardwood or shrub species. Our results clearly demonstrate that the stems of hardwood tree species and *A. incana* were selected over softwoods in our study areas. *T. occidentalis* seedling browsing incidence ranged from only 2.2% to 5.3% (of total) in the hare, moose, and higher deer harvest plot analyses, and it was only slightly greater at 8.6% in the designated cover plots. Browse on *T. occidentalis* saplings was likewise very low in the hare analysis at only 1.7%, yet ranged from 11.5% to 19.8% in the remaining analyses. Interestingly, perhaps due to overall higher browse pressure, frequency of browsed *T. occidentalis* saplings was roughly the same in the higher moose harvest plots as in the designated cover plots. *A. balsamea*, however, was selected much more over *T. occidentalis* in higher moose harvest plots.

In summary, our results do not suggest that browsing is a primary explanation for the poor *T. occidentalis* recruitment in these lowland stands, except perhaps in sites with habitat designated by the MDIFW as deer wintering areas. Though deer-yards clearly provide a valuable service to wildlife, and as such are protected from harvest, they may also exhibit the highest incidence of deer browse on *T. occidentalis* itself.

Finally, we recognize limitations in interpreting these results due to the uncertainties in the assumptions regarding ungulate population densities. The shift from greater deer densities to greater moose densities with increasing latitude is a widely accepted general trend in this region. In lieu of county-level or other regional population density estimates considered too coarse to use as a proxy for individual stands, we used town-level ungulate harvest data and stand-level DWA classifications. While harvest records for deer and moose may suggest relative species densities, harvest records are not typically sufficient for directly estimating population densities (Pettorelli

et al. 2007, Imperio et al. 2010). Likewise, the DWA designations at two of the study sites are unreliable predictors of actual deer winter use due to the lack of recent observations confirming the validity of the designations. Still, these may be regarded as useful indicators of habitat types particularly favorable for use as deer-yards. The analyses in this study were designed around these assumptions, but we note that each ungulate browse analysis likely reflects the combined browse selection of deer and moose, and there may be no difference in deer population densities or seasonal use between the higher deer harvest plots and the designated cover plots.

REFERENCES

Allen, T.J., 1970. Telemetry studies of deer movements and habitat utilization at Acadia National Park. M.S. thesis, University of Maine, Orono, Maine.

Baddeley, A., E. Rubak, and T. Turner, 2015. Spatial point patterns: Methodology and applications with R. Chapman and Hall/CRC Press, London.

Bates, D., M. Mächler, B., Bolker, and S. Walker, 2015. Fitting linear mixed-effects models using lme3. *Journal of Statistical Software 67*(1):1-48.

Beals, E.W., G. Cottam, and R.J. Vogl, 1960. Influence of deer on vegetation of the Apostle Islands, Wisconsin. *The Journal of Wildlife Management 24*(1):68-80.

Beatty, S.W., 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. *Ecology 65*(5):1406-1419.

Berrill, J.-P. and C.M. Dagley, 2012. Geographic patterns and stand variables influencing growth and vigor of Populus tremuloides in the Sierra Nevada (USA). *ISRN Forestry 2012*.

Berrill, J.-P., C.M., Dagley, S.A. Coppeto, and S.E. Gross, 2017. Curtailing succession: Removing conifers enhances understory light and growth of young aspen in mixed stands around Lake Tahoe, California and Nevada, USA. *Forest Ecology and Management 400*:511-522.

Berven, K., 2011. U.S. Forest Service Northern Conifer Experimental Forests: Historical review and examples of silvicultural research applications. Master's Thesis, University of Maine.

Berven, K., 2009. U.S. Forest Service Northern Conifer Experimental Forests: historical review and examples of silvicultural research applications. M.S. Thesis, University of Maine, Orono, Maine.

Boulfroy, E., E. Forget, P.V. Hofmeyer, L.S. Kenefic, C. Larouche, G. Lessard, J.-M. Lussier, F. Pinto, J.-C. Ruel, and A. Weiskittel, 2012. Silvicultural Guide for Northern White-Cedar (Eastern White Cedar). U.S.D.A. Forest Service. General Technical Report NRS-98. Northern Research Station. Newtown Square, PA, USA.

Bradshaw, L. and D.M. Waller, 2016. Impacts of white-tailed deer on regional patterns of forest tree recruitment. *Forest Ecology and Management 375*:1-11.

Burnham, K.P., and D.R. Anderson, 2003. Model selection and multimodel inference: A practical information-theoretic approach. Springer Science & Business Media, New York.

Caulkins, H.L., 1967. The ecology and reproduction of northern white-cedar. M.S. Thesis, School of Natural Resources, University of Michigan, Ann Arbor, Michigan.

Chimner, R.A. and J.B. Hart, 1996. Hydrology and microtopography effects on northern white-cedar regeneration in Michigan's Upper Peninsula. *Can. J. For. Res. 26*:389-393.

Choe, H.-M., M. Kim, and E.-K. Lee, 2017. The analysis of variance with the expected mean squares and its shiny application. *The R Journal 9*(1):252-261.

Conroy, M.J., L.W. Gysel, and G.R. Dudderar, 1979. Habitat components of clear-cut areas for snowshoe hares in Michigan. *The Journal of Wildlife Management 43*(3):680-690.

Coomes, D.A. and R.B Allen, 2007. Mortality and tree-size distributions in natural mixed-age forests. *Journal of Ecology 95*(1):27–40.

Cornett, M.W., P.B. Reich, and K.J. Puettmann, 1997. Canopy feedbacks and microtopography regulate conifer seedling distribution in two Minnesota conifer-deciduous forests. *Écoscience 4*(3):353-364.

Cornett, M.W., L.E. Frelich, K.J. Puettmann, and P.B. Reich, 2000. Conservation implications of browsing by *Odocoileus virginianus* in remnant upland *Thuja occidentalis* forest. *Biological Conservation 93*:359-369.

Crawford, H.S., 1982. Seasonal food selection and digestibility by tame white-tailed deer in central Maine. *The Journal of Wildlife Management 46*(4):974-982.

Curtis, J.D., 1946. Preliminary observations on northern white cedar in Maine. *Ecology 27*(1):23-36.

Daniels, R.F. and H.E. Burkhart, 1975. Simulation of individual tree growth and stand development in managed loblolly pine plantations. Div. For. Wild. Res., Virginia Polytechnic and State University, Blacksburg, VA, FWS-5-75, 69pp.

Dey, D.C., B.O. Knapp, M.A. Battaglia, R.L. Deal, J.L. Hart, K.L. O'Hara, C.J. Schweitzer, and T.M. Schuler, 2019. Barriers to natural regeneration in temperate forests across the USA. *New forests 50*(1):11-40.

Diamond, J.S., D.L. McLaughlin, R.A. Slesak, and A. Stovall, 2020. Microtopography is a fundamental organizing structure of vegetation and soil chemistry in black ash wetlands. *Biogeosciences 17*:901–915.

Ditchkoff, S.S., and F.A. Servello, 1998. Litterfall: an overlooked food source for wintering white-tailed deer. *The Journal of Wildlife Management 62*(1):250-255.

Duchesneau, R., I. Lesage, C. Messier, and H. Morin, 2001. Effects of light and intraspecific competition on growth and crown morphology of two size classes of understory balsam fir saplings. *Forest Ecology and Management 140*:215-225.

Dumont, A., J.-P. Ouellet, M. Crête, and J. Huot, 2005. Winter foraging strategy of white-tailed deer at the northern limit of its range. *Écoscience 12*(4):476-484.

Enquist, B.J., G.B. West, E.L. Charnov, and J.H. Brown, 1999. Allometric scaling of production and life history variation in vascular plants. *Nature 401*:907–911.

Fraver, S., A.S. White, and R.S. Seymour, 2009. Natural disturbance in an old-growth landscape of northern Maine, USA. *Journal of Ecology 97*(2):289-298.

Fraver, S., A.M. Milo, J.B. Bradford, A.W. D'Amato, L. Kenefic, B.J. Palik, C.W. Woodall, and J. Brissette, 2013. Woody debris volume depletion through decay: Implications for biomass and carbon accounting. *Ecosystems 16*(7):1262-1272

Fraver, S., M.J. Ducey, C.W. Woodall, A.W. D'Amato, A.M. Milo, and B.J. Palik, 2018. Influence of transect length and downed woody debris abundance on precision of the line-intersect sampling method. *Forest Ecosystems 5*:39.

Fraver, S., L.S. Kenefic, A.R. Cutko, and A.S. White, 2020. Natural disturbance and stand structure of old-growth northern white-cedar (Thuja occidentalis) forests, northern Maine, USA. *Forest Ecology and Management 456*:117680

Frazer, G.W., C.D. Canham, and K.P. Lertzman, 1999. Gap Light Analyzer (GLA), Version 2.0: User's manual and program documentation.

Frelich, L.E. and C.G. Lorimer, 1985. Current and predicted long-term effects of deer browsing in hemlock forests in Michigan, USA. *Biological Conservation 34*:99-120.

Frelich, L.E. and C.G. Lorimer, 1991. Natural disturbance regimes in hemlock-hardwood forests of the upper Great Lakes region. *Ecological monographs 61*(2):145-164.

Forester, J.D., D.P. Anderson, and M.G. Turner, 2008. Landscape and local factors affecting northern white cedar (*Thuja occidentalis*) recruitment in the Chequamegon-Nicolet National Forest, Wisconsin (U.S.A.). *Am. Midl. Nat. 160*:438-453.

Fuller, A.K., and D.J. Harrison, 2009. Home range, habitat use, edge relationships, mortality sources, age structures, and survival of white-tailed deer on Mount Desert Islands, Maine, 1992-1994. Contract Report, Natural Resources Stewardship Science Office Northeast Region, U.S. National Park Service.

Gawler, S., and A. Cutko, 2010. Natural landscape of Maine: A guide to natural communities and ecosystems. Maine Natural Areas Program, Maine Department of Conservation, Augusta, Maine.

Geniusz, M.S., 2015. Plants have so much to give us, all we have to do is ask. University of Minnesota Press. Minneapolis, Minnesota, USA.

Gräler, B., E. Pebesma, and G. Heuvelink, 2016. Spatio-temporal interpolation using gstat. *The R Journal 8*:204-218.

Haase, P., 1995. Spatial pattern analysis in ecology based on Ripley's K-function: Introduction and methods of edge correction. *Journal of Vegetation Science 6*(4):575–582.

Hegyi, F., 1974. A simulation model for managing jack-pine stands. In: Fries, J. (ed.) Growth models for tree and stand simulations, pp. 74–90. Royal College of Forestry, Research Notes 30, Uppsala, SE.

Heinze, G., C. Wallisch, and D. Dunkler, 2018. Variable selection – A review and recommendations for the practicing statistician. *Biometrical Journal 60*(3):431-449.

Heitzman, E., K.S. Pregitzer, and R.O. Miller, 1997. Origin and early development of northern white-cedar stands in northern Michigan. *Can. J. For. Res. 27*:1953-1961.

Heitzman, E., K.S. Pregitzer, R.O. Miller, M. Lanasa, and M. Zuidema, 1999. Establishment and development of northern white-cedar following strip clearcutting. *Forest Ecology and Management 123*:97-104.

Hodgkins, G.A., and R.W. Dudley, 2006. Changes in late-winter snowpack depth, water equivalent, and density in Maine, 1926-2004. *Hydrol. Process. 20*:741-751.

Hofmeyer, P.V., L.S. Kenefic, and R.S. Seymour, 2009. Northern white-cedar ecology and silviculture in the northeastern United States and southeastern Canada: A synthesis of Knowledge. *Northern Journal of Applied Forestry 26*(1):21-27.

Imperio, S., M. Ferrante, A. Grignetti, G. Santini, and S. Focardi, 2010. Investigating population dynamics in ungulates: do hunting statistics make up a good index of population abundance? *Wildlife Biology* 16(2):205-214.

Jakubas, W., and R. Cross, 2002. Snowshoe are (Lepus americanus) Assessment 2001. MDIFW Wildlife Resources Assessment Section.

Johnston, W.F., 1977. Northern white-cedar in the north central states. General technical report NC-35. U.S. Forest Service North Central Forest Experiment Station.

Johnston, W.F., 1990. *Thuja occidentalis* L. northern white-cedar. Pages 580-589 *in* R. M. Burns, and B.H. Honkala, editors. Silvics of North America Volume 1, Conifers. Forest Service, U.S.D.A. Agricultural Handbook 654. Washington, DC, USA.

Kangas, L.C., R. Schwartz, M.R. Pennington, C.R. Webster, and R.A. Chimner, 2016. Artificial microtopography and herbivory protection facilitates wetland tree (*Thuja occidentalis* L.) survival and growth in created wetlands. *New Forests 47*:73-86.

Kearney, S.R. and F.F. Gilbert, 1976. Habitat use by white-tailed deer and moose on sympatric range. *The Journal of Wildlife Management 40*(4):645-657.

Kenkel, N.C., 1988. Pattern of self-thinning in jack pine: Testing the random mortality hypothesis. *Ecology 69*(4):1017-1024.

Kneeshaw, D.D., and Y. Bergeron, 1996. Ecological factors affecting the abundance of advance regeneration in Quebec's southwestern boreal forest. *Can. J. For. Res 26*:888-898.

Larouche, C., L.S. Kenefic, and J.-C. Ruel, 2010. Northern white-cedar regeneration dynamics on the Penobscot Experimental Forest in Maine: 40-Year Results. *North. J. Appl. For. 27*(1):5-12.

Larouche, C., J.-C. Ruel, and J.-M. Lussier, 2011. Factors affecting northern white-cedar (*Thuja occidentalis*) seedling establishment and early growth in mixedwood stands. *Can. J. For. Res. 41*:568-582.

Larouche, C. and J.-C. Ruel, 2015. Development of northern white-cedar regeneration following partial cutting, with and without deer browsing. *Forests 6*:344-359.

Lorimer, C.G., 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. *Forest Ecology and Management 6*:343-360.

Ludewig, H.A. and R.T. Bowyer, 1985. Overlap in winter diets of sympatric moose and white-tailed deer in Maine. *Journal of Mammology 66*(2):390-392.

Maine Department of Inland Fisheries and Wildlife, and Wildlife Hub, 2019. Deer Wintering Area data set. Accessed on July 25, 2020 at URL https://hub.arcgis.com/datasets/maine::maine-deer-wintering-areas.

Maine Department of Inland Fisheries and Wildlife, 2019. Harvest Reports. Accessed July 25, 2020 at URL https://www.maine.gov/ifw/hunting-trapping/harvest-information.html.

Maine Geological Survey, 2020. Maine Cooperative Snow Survey Data, 2017-2019. Accessed November 5, 2020 at URL https://www.maine.gov/dacf/mgs/hazards/snow_survey/.

Miller, K.M., and B.J. McGill, 2019. Compounding human stressors cause major regeneration debt in over half of eastern US forests. *Journal of Applied Ecology 56*(6):1-12.

Nelson, T.C., 1951. A reproduction study of northern white cedar. Thesis, Michigan State College of Agriculture and Applied Science, East Lansing, Michigan, USA.

Nicotra, A.B., R.L. Chazdon, and S.V.B. Iriarte, 1999. Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology 80*(6):1908-1926.

Oliver, C.D. and B.C. Larson, 1996. Forest Stand Dynamics, Update Edition. John Wiley & Sons, Inc., New York. 520 p.

Pettorelli, N., S.D. Côté, A. Gingras, F. Potvin, and J. Huot, 2007. Aerial surveys vs hunting statistics to monitor deer density: the example of Anitcosti Islands, Quebec, Canada. *Wildlife Biology* 13(3):321-327.

Pierson, T.G., and D.S. DeCalesta, 2015. Methodology for estimating deer browsing impact. *Human-Wildlife Interactions 9*(1):67-77.

Poznanovic, S.K., A.J. Poznanovic, C.R. Webster, and J.K. Bump, 2014. Spatial patterning of underrepresented tree species in canopy gaps 9 years after group selection cutting. *Forest Ecology and Management 331*:1-11.

Pregitzer, K.S., 1990. The ecology of northern white-cedar. In: Northern white-cedar in Michigan, Workshop Proceedings. Agricultural Experiment Station Research Report. Volume 512:8–14.

PRISM Climate Group, Oregon State University, 2020. 30 Year Normals data set. Accessed May 25, 2020 at URL http://prism.oregonstate.edu.

Reuling, L.F., C.C. Kern, L.S. Kenefic, and D.R. Bronson, 2019. The northern white-cedar recruitment bottleneck: understanding the effects of substrate, competition, and deer browsing. *Forests 10*(501).

Rice, J.M., C.B. Halpern, J.A. Antos, and J.A. Jones, 2012. Spatio-temporal patterns of tree establishment are indicative of biotic interactions during early invasion of a montane meadow. *Plant Ecology 213*:555-568.

Ripley, B.D., 1977. Modelling spatial patterns. *J. R. Stat. Soc. B 39*:172-212

Rooney, T.P., S.L. Solheim, and D.M. Waller, 2002. Factors affecting the regeneration of northern white cedar in lowland forests of the Upper Great Lakes region, USA. *Forest Ecology and Management 163*:119-130.

Routledge, R.G., and J. Roese, 2004. Moose winter diet selection in central Ontario. *Alces 40*:95-101.

Ruel, J.-C., J.-M. Lussier, S. Morissette, and N. Ricodeau, 2014. Growth response of northern white-cedar (*Thuja occidentalis*) to natural disturbances and partial cuts in mixedwood stands of Quebec, Canada. *Forests* 5:1194-1211.

Saucier, L., J.-C. Ruel, and C. Larouche, 2018. Variations in northern white-cedar (*Thuja occidentalis*) regeneration following operational selection cutting in mixedwood stands of western Quebec. *Can. J. For. Res. 48*:1311-1319.

Scott, M.L. and P.G. Murphy, 1987. Regeneration patterns of northern white cedar, an old-growth forest dominant. *The American Midland Naturalist 117*(1):10-16.

Silla, F., S. Fraver, A. Lara, T.R. Allnutt, and A. Newton, 2002. Regeneration and stand dynamics of *Fitzroya cupressoides* (Cupressaceae) forests of southern Chile's Central Depression. *Forest Ecology and Management*, *165*(1-3), pp.213-224.

Sollins, P., 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. *Can. J. For. Res. 12*:18–28.

St. Hilaire, L.R. and D.J. Leopold, 1995. Conifer seedling distribution in relation to microsite conditions in a central New York forested minerotrophic peatland. *Can. J. For. Res. 25*:261-269.

Tefler, E.S., 1972. Browse selection by deer and hares. *The Journal of Wildlife Management 36*(4):1344-1349.

Thiele, C. and G. Hirschfeld, 2020. Cutpointr: Improved estimation and validation of optimal cutpoints in R. Journal of Statistical Software. https://arxiv.org/abs/2002.09209

Thompson, M.E., J.R., Gilbert, G.J. Matula, Jr., and K.I. Morris, 1995. Seasonal habitat use by moose on managed forest lands in northern Maine. *Alces 31*:233-245.

Thompson, E.H. and E.R. Sorenson, 2005. Wetland, woodland, wildland: A guide to the natural communities of Vermont. University Press of New England. Lebanon, New Hampshire, USA.

U.S. Census Bureau, 2010. Gazetteer Files. Accessed November 3, 2020 at URL https://www.census.gov/geographies/reference-files/time-series/geo/gazetteer-files.2010.html.

U.S. Fish and Wildlife, 2013. Sunkhaze Meadows National Wildlife Refuge and Carlton Pond Waterfowl Production Area comprehensive conservation plan. Accessed November 14, 2020 at URL https://www.fws.gov/refuge/Sunkhaze_Meadows/what_we_do/finalccp.html.

U.S. Geological Survey, 2018. The National Map. Accessed May 25, 2020 at URL https://viewer.nationalmap.gov/advanced-viewer/.

Van Wagner, C.E., 1968. The line intersect method in forest fuel sampling. *For Sci 14*(1):20–26.

Verme, L.J., and W.F. Johnston, 1986. Regeneration of northern white-cedar deeryards in upper Michigan. *The Journal of Wildlife Management 50*(2):307-313.

Villemaire-Côté, O., J.-C. Ruel, and L. Sirois, 2017. Development of northern white-cedar (*Thuja occidentalis* L.) plantations within and outside deer yards. *Forests 8*(326).

Web Soil Survey, Natural Resources Conservation Service, US Department of Agriculture, 2020. Accessed May 21, 2020 at URL http://websoilsurvey.nrcs.usda.gov/.

Wesely, N., S. Fraver, L.S. Kenefic, A.R. Weiskittel, J.-C. Ruel, M.E. Thompson, and A.S. White, 2018. Structural attributes of old-growth and partially harvested northern white-cedar stands in northeastern North America. *Forests 9*(376).

White, M.A., 2012. Long-term effects of deer browsing: composition, structure, and productivity in a northeastern Minnesota old-growth forest. Forest Ecology and Management. 269:222-228.

Wickham, H., 2016. Ggplot2: Elegant graphics for data analysis. Springer-Verlag New York.

APPENDIX

Table 12. Study site ownership.

Site	Ownership
Acadia National Park	US National Park Service
Big Reed Forest Reserve	The Nature Conservancy
Moosehorn National Wildlife Refuge	US Fish and Wildlife Service
Penobscot Experimental Forest	US Forest Service, Univ. of Maine Foundation
Sunkhaze Meadows National Wildlife Refuge	US Fish and Wildlife Service

Figure 10. Examples of stem browse. Ungulate (left) and hare browse (right) on the current year's stems of cedar seedlings. These examples illustrate typical browse observed during field sampling.

Table 13. Vigorous vs suppressed sapling model summary. Results of a binomial model using diameter at breast height and live crown ratio to predict if an individual in the sapling size class is a vigorous or suppressed sapling. A random subset of data (N=632) containing individuals noted in the field as vigorous or suppressed was used to train the model. The model demonstrates that observations made in the field reliably differentiated between two morphological types based on size and vigor (inferred through LCR), i.e., greater DBH was associated with suppressed stems and greater LCR was associated with vigorous saplings.

(vigorous/suppressed sapling) ~ DBH + ln(LCR), family = binomial

Variable	df	Estimate	*P*-value
DBH	1	-1.14	<0.001
lnLCR	1	3.84	<0.001

$R^2 = 0.802$, N=632

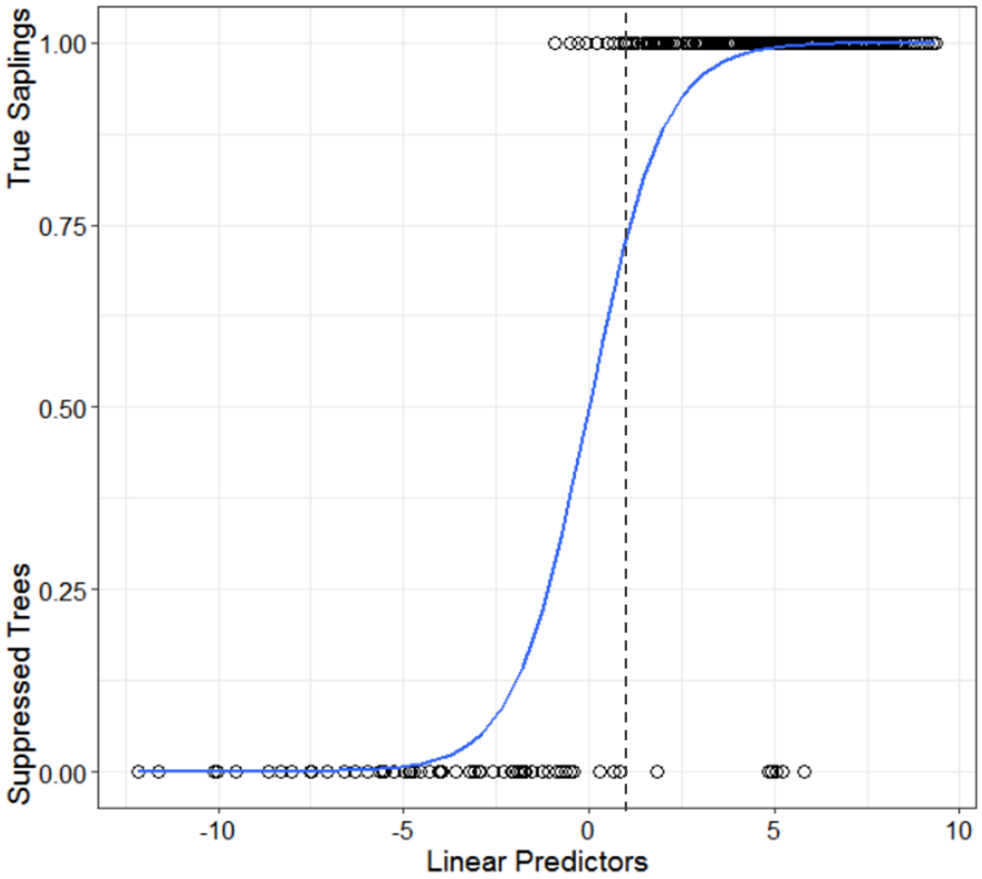

Figure 11. Vigorous vs suppressed sapling model results. This binomial model predicts if an individual in the sapling size class is a vigorous or suppressed sapling (as judged during field sampling), where linear predictors are a function of DBH and live crown ratio. A random subsample of field data was used to train the model (training subset N=632). The vertical dashed line represents the cutpoint calculated based on optimal sensitivity and selectivity (cutpoint = 0.856). Applying this cutpoint to the remaining individuals in the sapling size class (validation subset N=632) correctly predicted the identity of 98% of records.

Table 14. Crown projection area equations. Crown projection area (CPA, m^2) is predicted from diameter at breast height (DBH, cm). N, number of trees on which equations are based; RMSE, root mean square error.

Size Class	Species	N	DBH range (cm)	Equation	R^2	RMSE
Trees	*Abies balsamea*	79	10.0 - 43.2	ln(CPA) = -0.50983 + 1.01198 * ln(DBH)	0.42	0.40
	Acer rubrum	60	10.0 - 42.0	ln(CPA) = -0.06147 + 0.94767 * ln(DBH)	0.27	0.54
	Betula alleghaniensis	41	10.5 - 80.5	ln(CPA) = 0.56594 + 1.00599 * ln(DBH)	0.78	0.32
	Betula papyrifera	31	10.1 - 48.5	ln(CPA) = -1.22099 + 1.29813 * ln(DBH)	0.56	0.48
	Fraxinus nigra	42	10.0 - 50.7	ln(CPA) = -1.36836 + 1.24478 * ln(DBH)	0.61	0.44
	Larix laricina	19	13.0 - 59.8	ln(CPA) = -2.81760 + 1.60262 * ln(DBH)	0.66	0.47
	Picea rubens	641	10.1 - 62.0	ln(CPA) = -1.48420 + 1.25770 * ln(DBH)	0.53	0.47
	Pinus strobus	64	10.8 - 78.8	ln(CPA) = -2.68237 + 1.67892 * ln(DBH)	0.83	0.36
	Thuja occidentalis	111	10.1 - 77.8	ln(CPA) = -1.44921 + 1.20219 * ln(DBH)	0.62	0.43
	Tsuga canadensis	88	10.6 - 67.8	ln(CPA) = -1.06719 + 1.24139 * ln(DBH)	0.54	0.45
Saplings	*Abies balsamea*	20	0.6 - 10.0	ln(CPA) = -0.15759 + 0.71887 * ln(DBH)	0.60	0.53
	Acer rubrum	19	0.4 - 9.4	ln(CPA) = -0.65747 + 1.37619 * ln(DBH)	0.85	0.53
	Betula alleghaniensis	12	0.5 - 9.8	ln(CPA) = -0.11527 + 1.17522 * ln(DBH)	0.76	0.66
	Fraxinus nigra	18	0.6 - 7.8	ln(CPA) = -0.72194 + 1.20601 * ln(DBH)	0.86	0.35
	Larix laricina	11	0.8 - 8.7	ln(CPA) = -0.83810 + 1.04574 * ln(DBH)	0.83	0.39
	Picea rubens	15	0.7 - 9.8	ln(CPA) = 0.10273 + 0.56582 * ln(DBH)	0.41	0.49
	Pinus strobus	11	0.4 - 9.7	ln(CPA) = -0.92975 + 1.28935 * ln(DBH)	0.89	0.44
	Thuja occidentalis	24	0.3 - 8.9	ln(CPA) = -0.15723 + 0.57385 * ln(DBH)	0.80	0.35
	Tsuga canadensis	16	0.5 - 10.0	ln(CPA) = -0.52224 + 1.17581 * ln(DBH)	0.84	0.60

Table 15. Overstory species relative basal area (%). All 15 stands are shown with species ranked from highest to lowest overall relative basal area (averaged across stands).

Species	ANP1	ANP2	ANP3	BR1	BR2	BR3	MH1	MH2	MH3	PEF1	PEF2	PEF3	SM1	SM2	SM3
Thuja occidentalis	85.9	88.7	78.9	91.8	93.9	81.1	86.8	92.3	68.9	93.4	68.1	67.0	82.1	85.3	78.0
Picea rubens	3.2	8.7	0.5	4.4	1.6	4.5	1.1	1.9	6.6	4.0	8.4	16.3	16.4	7.8	2.1
Acer rubrum	1.9	0.4	6.9	-	-	1.0	5.1	-	6.3	-	14.8	15.2	-	-	-
Abies balsamea	-	0.8	0.3	3.2	2.1	6.0	4.7	0.8	6.5	0.5	4.6	-	0.8	3.3	5.1
Tsuga canadensis	-	-	-	-	-	-	-	-	-	-	0.6	-	0.8	2.4	14.5
Pinus strobus	-	-	12.1	-	-	-	-	-	4.4	-	-	-	-	-	-
Betula papyrifera	-	0.9	-	-	-	1.6	1.3	3.6	6.8	-	0.1	-	-	1.1	0.3
Betula alleghaniensis	1.6	0.3	1.3	-	2.1	1.6	1.1	1.3	0.7	-	0.8	-	-	-	-
Larix laricina	7.3	-	-	-	-	-	-	-	-	-	-	1.5	-	-	-
Fraxinus nigra	-	0.2	-	0.3	-	4.2	-	0.3	-	0.8	2.5	-	-	-	-
Picea glauca	-	-	-	-	-	-	-	-	-	1.3	-	-	-	-	-
Betula cordifolia	-	-	-	0.3	0.4	-	-	-	-	-	-	-	-	-	-

Table 16. Sapling species tally. All 15 plots are shown, with tallies based on live saplings of tree species in the 15 × 15 m interior plot only. Species ranked from highest to lowest overall abundance (averaged across stands).

Species	ANP1	ANP2	ANP3	BR1	BR2	BR3	MH1	MH2	MH3	PEF1	PEF2	PEF3	SM1	SM2	SM3
Abies balsamea	1	-	-	36	5	21	4	70	3	32	59	6	241	176	85
Thuja occidentalis	-	3	14	42	18	22	-	30	22	-	-	3	11	15	-
Alnus incana	-	-	16	34	1	27	-	-	-	1	2	-	-	-	-
Fraxinus nigra	-	-	-	32	-	19	-	6	-	4	4	-	2	-	1
Picea rubens	4	1	5	17	8	5	-	1	-	-	9	-	-	-	-
Tsuga canadensis	-	-	-	-	-	-	-	-	-	-	5	-	1	-	21
Betula alleghaniensis	-	-	-	7	10	6	-	-	-	-	3	-	-	-	-
Ilex verticillata	-	-	-	-	-	-	-	-	-	2	3	11	1	1	-
Larix laricina	-	-	14	-	-	-	-	-	-	-	-	-	-	-	-
Acer pensylvanicum	-	-	-	3	-	4	-	-	-	-	-	-	-	-	-
Acer rubrum	-	1	1	1	-	1	-	-	-	-	-	-	-	2	-
Pinus strobus	1	-	-	1	-	-	-	-	-	-	-	-	1	2	-

Table 17. Seedling species tally. All 15 plots, with tallies based on live seedlings of tree species in the 15 × 15 m interior plot only. Species ranked from highest to lowest overall relative abundance (averaged across stands).

Species	ANP1	ANP2	ANP3	BR1	BR2	BR3	MH1	MH2	MH3	PEF1	PEF2	PEF3	SM1	SM2	SM3
Thuja occidentalis	1668	254	1764	958	289	885	142	440	378	28	77	67	543	419	172
Abies balsamea	36	28	3	75	79	56	8	95	62	358	139	105	120	425	151
Acer rubrum	5	3	6	11	9	69	18	254	36	44	4	111	23	83	77
Picea rubens	258	82	59	58	15	22	-	8	-	5	4	27	4	19	5
Larix laricina	158	18	69	-	-	-	-	-	-	-	-	6	-	-	-
Tsuga canadensis	-	-	-	-	-	-	-	1	-	-	16	9	5	1	116
Fraxinus nigra	-	1	-	16	-	7	2	59	-	5	9	1	2	1	-
Betula alleghaniensis	1	-	-	14	4	34	2	-	-	-	2	-	1	-	-
Pinus strobus	4	2	10	-	1	1	-	1	-	-	1	6	1	1	-
Acer saccharum	-	-	-	7	12	4	-	-	-	-	-	-	-	-	2
Acer pensylvanicum	-	1	-	4	4	3	-	-	-	-	-	-	-	-	-
Amelanchier spp.	-	-	-	-	-	-	-	-	1	-	-	1	1	5	-
Betula papyrifera	1	-	2	-	-	-	-	-	-	-	-	3	-	2	-
Sorbus spp.	-	-	-	1	1	3	-	-	-	-	-	-	-	2	-
Fagus grandifolia	-	-	-	-	-	-	-	-	-	-	2	-	2	-	-
Quercus rubra	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-
Betula cordifolia	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-
Rhamnus cathartica	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-

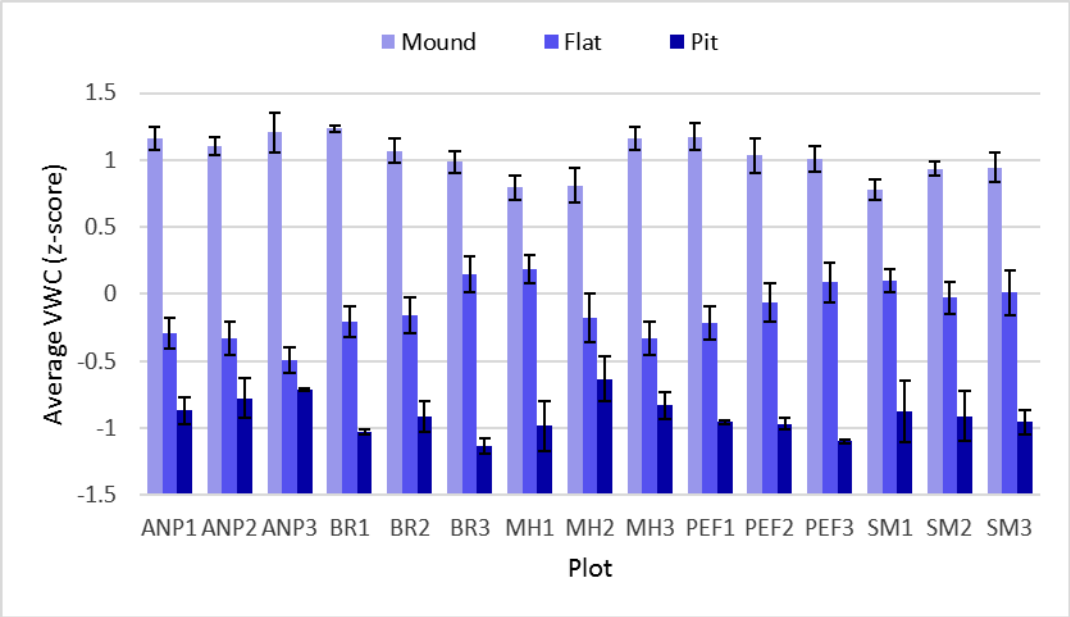

Figure 12. Average soil moisture by plot. Averages of 25 mounds, 25 flats, and 25 pits at each of 15 plots. Soil moisture is expressed as a plot-level z-score of volumetric water content, where a greater z-score equates to lower moisture. Error bars represent one standard error. While the discrepancies in moisture between the three microtopographic features differ by plot, the same trend is observed at all plots: flats are wetter than mounds, and pits are wetter than flats.

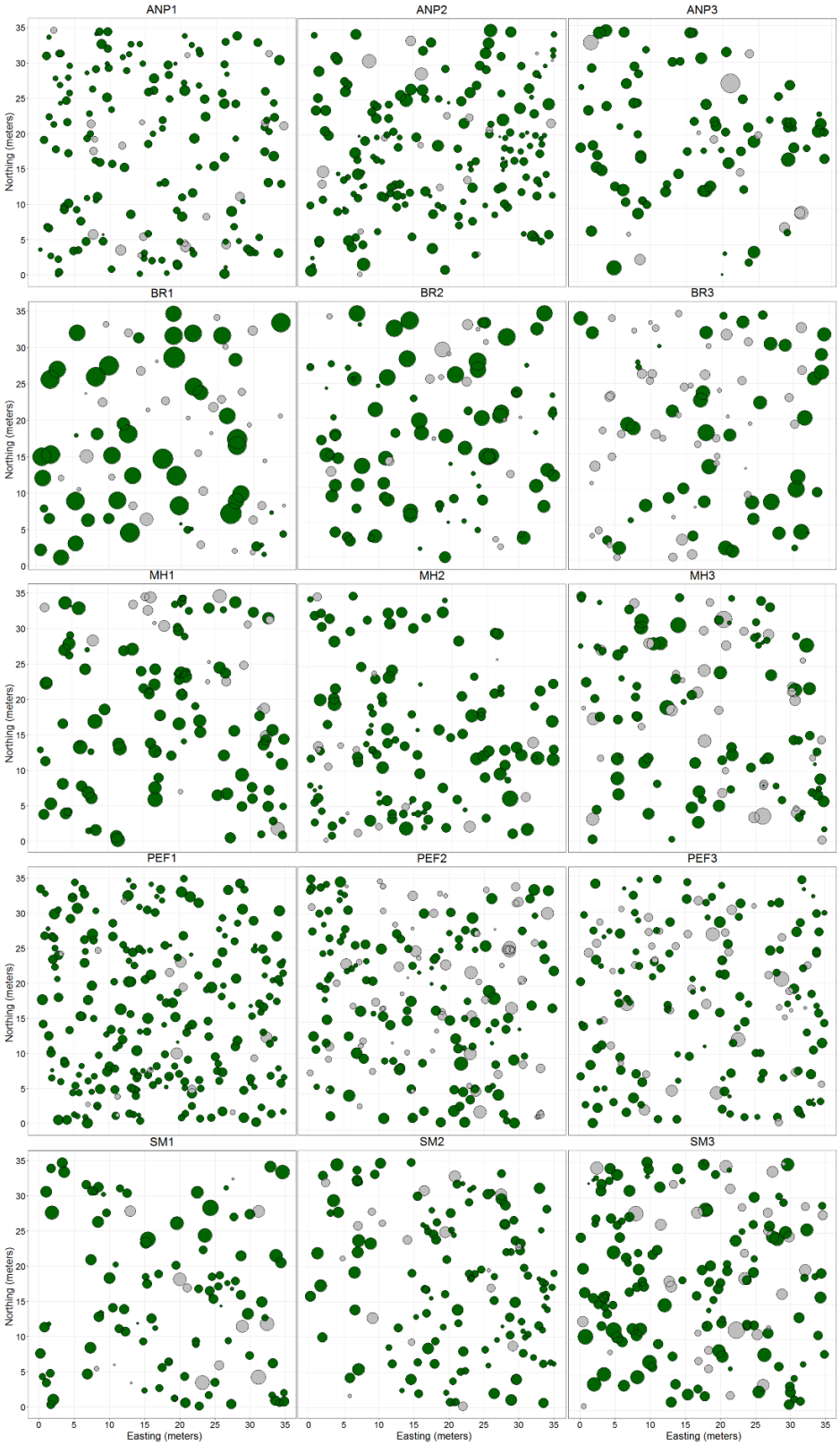

Figure 13. Overstory stem maps. Live trees at all plots are shown. Cedars are in dark green, and other species are in light grey. Size of points reflect relative tree diameters (standardized across plots), but these are not to scale relative to plot.

BIOGRAPHY OF THE AUTHOR

Jeanette Allogio was born in Vernon, NJ. After graduating from Vernon Township High School she earned a Bachelor of Science degree in Ecology and Natural Resources from Rutgers University School of Environmental and Biological Sciences in 2010. As a student she taught species identification as a dendrology lab instructor and assisted her academic advisor, Dr. Lena Struwe, in her research on the taxonomy of ring gentians. During this time, Jeanette discovered her interest in field botany and a desire to work in the discipline plant ecology.

Following graduation Jeanette worked as a field and lab technician in as many different roles and ecosystems as possible. This work included supporting the range monitoring and restoration efforts of the Bureau of Land Management, land use monitoring and rehabilitation of military training lands, and assisting researchers with the National Park Service and the Jones Ecological Research Center. Through these positions she learned the importance of incorporating science-based methods into effective conservation and land management strategies, so she decided to pursue a forest ecology degree to promote this principle. Jeanette is a candidate for the Master of Science degree in Forest Resources from the University of Maine in December 2020.